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JARMILA KUBÍKOVÁ, JOSEF RUSEK

Development of xerothermic rendzinas

A study in ecology and soil microstructure

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Řídí člen korespondent ČSAV Jaroslav Purš
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1. INTRODUCTION

At present a great number of studies in ecology, botany, zoology, soil microbiology etc. exist which try to characterize a certain part of nature by species ennumerations, descriptions of ecotope, results of different measurements, results of chemical analysis, by coenotical relations, life forms, seasonal dynamics and migrations, and other characteristics. The majority of these studies suffer from the limited view of one specialist to the selected problem, covering only a small part of the great species diversity of plants, animals and microbes with little regard to their interactions within the studied ecotope.

In recent years, the ecologists of the whole world are becoming more and more aware of the necessity of complex nature research; this new conception has resulted in the effort to organize great international programmes. In many countries as well as in Czechoslovakia teams of specialists were organized who following the intentions of International Biological Programme (IBP) studied primary and secondary production of chosen habitats, e. g. at the pond Nesyt in Moravia, in the forest Báb in Slovakia, in the forest complex Solling in BRD etc. These are long-term researches which need careful methodical preparation.

In our study, we aimed at elucidating the seasonal dynamics of plants, microbes and zooedaphon related to the changes of their biotope. Especially we were interested in the interrelations of the biota and soil development. To fulfil this programme, several conditions were necessary. Firstly, a suitable locality had to be found. The selected locality had to be relatively untouched by human activity, a part of a well known district and not very far from Prague where our Institutes were situated. The area of Bohemian Karst, 40 km SW from Prague fulfilled all these conditions most satisfactorily.

The area of Bohemian Karst has been a frequent venue for naturalists excursions for more than 150 years. That was also the reason, why one of the well known localities, Velká hora hill by Srbsko was chosen for the first czech collective study, organized by prof. J. Klika in the years 1935 to 1940 (KLIKA 1942). The idea of complex ecosystem study appeared also in a series of theses from the Department of Botany, Charles University, Prague, worked out in the years 1958 to 1960 (STRNADOVÁ 1959, SMETÁNKOVÁ 1959, CHOCHOLOVÁ 1960, PACHNEROVÁ 1960, KUČEROVÁ 1960). In these works, supervised by doc. J. Jeník, the main accent was put on detailed measurements of different ecological factors and on autecology of selected plant species on Velká hora hill and Doutnáč hill. These studies were followed by synecological study of JANKO (1965) and by the research in soil fungi (FASSATIOVÁ 1966).

As a model site for this study the southern slope of the hill Doutnáč was chosen; its profile diagram may be seen on Fig. 1.

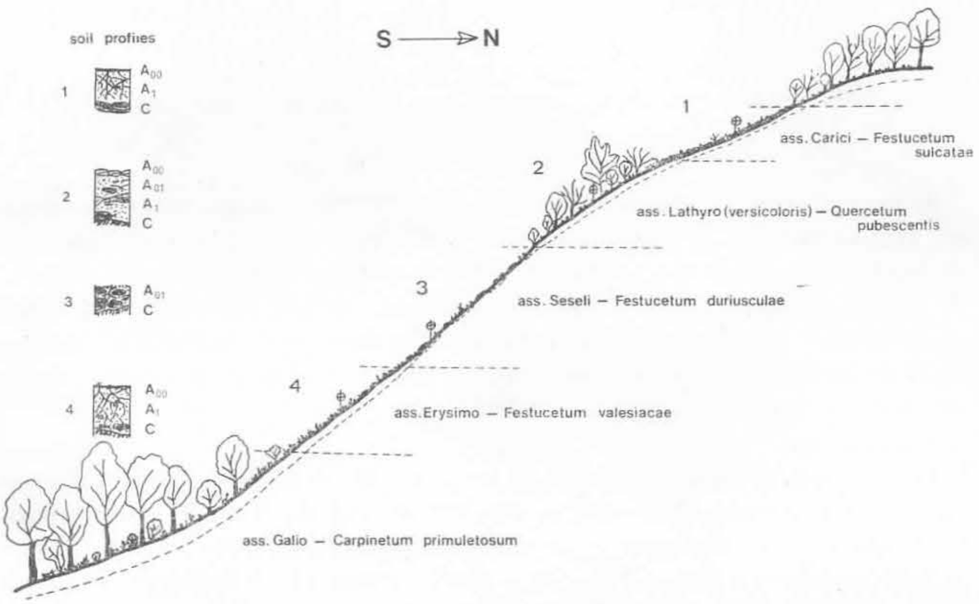
soil profiles
S ⟶ N
1 A_{00} A_1 C
2 A_{00} A_{01} A_1 C
3 A_{01} C
4 A_{00} A_1 C
1
ass. Carici – Festucetum sulcatae
2
ass. Lathyro (versicoloris) – Quercetum pubescentis
3
ass. Seseli – Festucetum duriusculae
4
ass. Erysimo – Festucetum valesiacae
ass. Galio – Carpinetum primuletosum

Fig. 1. Profile of the southern slope of Doutnáč hill showing the distribution of ecotopes, plant communities and soil profiles.

Other basic requirements for the successful fulfilment of our programme were the methods used. Their selection was limited by our special field of research and by the equipment of our Institutes. Thus it so happened that some parts of the ecosystem were studied in greater detail than others. For instance the species composition of soil fungi and bacteria could not be studied in detail. Some results of soil fungi were taken from the previous work by FASSATIOVÁ (1966). From all groups of soil fauna, only *Apterygota* were studied in detail up to the species level. Other soil *Arthropoda* were grouped on family or order level and the numbers of these groups are given. Soil macrofauna could be studied only in a preliminary way.

2. DESCRIPTION OF THE MODEL SITE

The hill Doutnáč in the Bohemian Karst was chosen as a model site. It lays on 14°06′E. l. and 49°58′N. lat., its peak being 428m above sea level.

The Bohemian Karst is an elliptical district between Zdice and Prague following the valley of river Berounka. This geographical district coincides with geological district Barrandian, formed by limestones, shales and diabases dated from older Palaeozoic.

The hill Doutnáč lays in the centre of Barrandian. Its slopes facing to East, South and West are steep with relative height about 100 m, to the North is the peak followed by a slowly lowering crest.

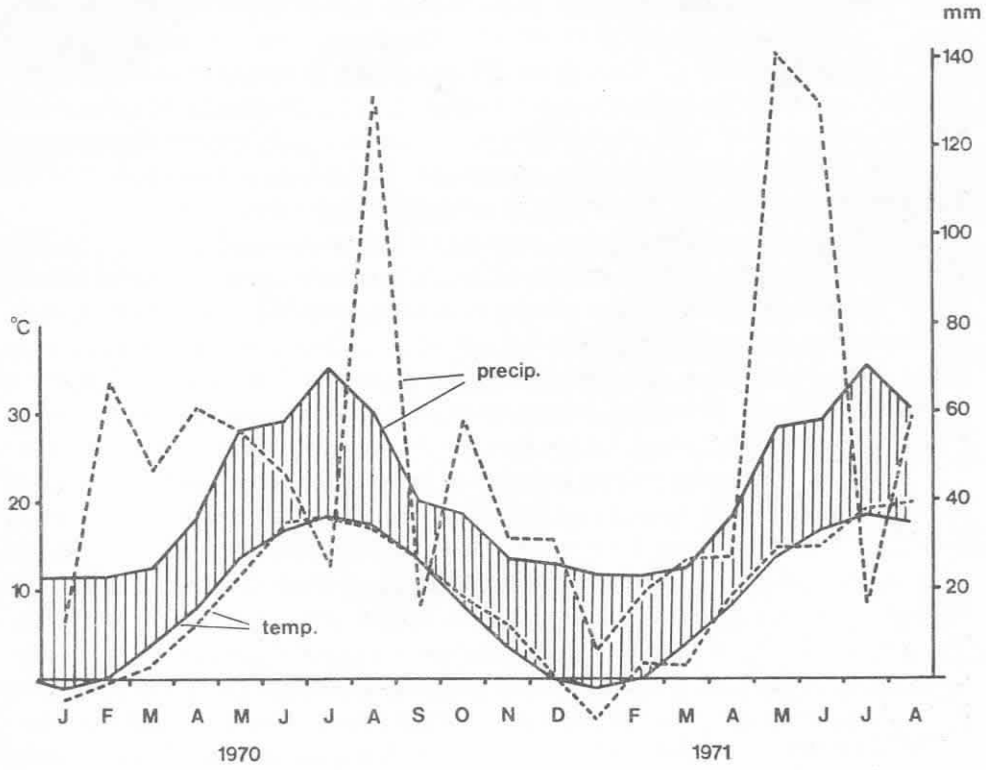

Fig. 2. Average month precipitation and temperature of the period studied plotted on the basis of climadiagram (50 year averages) show the differences of the studied period from the average.

The whole district of Bohemian Karst has been the bottom of a sea during the Silurian, and Devonian periods and different layers can be found here with little interruption. During the Upper Devonian and Lower Carbonian the area was transformed during Variscan orogeny. In that time a series of anticlines and synclines has developed. The studied hill Doutnáč is a part of an outstanding anticline going through Boubová hill, Doutnáč hill, Paní hora hill to the village Kozolupy. The inclination of layers is here greater on the southern slopes, smaller on northern slopes. On the southern slope of the hill Doutnáč is the direction of layers E – W and their inclination 25°, which results in a big plate parallel to the recent slope inclination. The hill is built of Silurian and Devonian limestones, and according to SVOBODA and PRANTL (1953, 1955), the older Silurian is on the top, in the middle of the hill begin the younger Devonian layers. The thermophilous ecotopes, occupied by grassland steppe occur as a rule on the upper third of the slope, thus occupying the Silurian limestone layers. The same situation may be found on other similar thermophilous localities.

The climate of the Bohemian Karst is, according to Atlas podnebí ČSR (VESECKÝ red., 1961) mildly warm, mildly dry mostly with a mild winter (district B_2). The climadiagram from the station Králův Dvůr characterizes the climate. The 50 year averages of monthly temperatures and precipitation were used and compared with actual conditions during the years 1970 to 1971. Great deviations may be seen, especially the marked dry period in summer (Fig. 2).

The limestone district of the Bohemian Karst differs in many aspects from neighbouring districts. Its steep slopes, deeply eroded canyons, limestone rocks alternating with volcanic diabases and alluvial sediments and its relatively dry, warm climate are the cause of very diversified ecotopes supporting the existence of many taxa of biota. There were conditions for the survival of relict species both from cold glacial periods (e. g. *Sesleria calcarea*) and from dry continental steppe dominating the beginning of Holocene (*Stipa* spp., *Koeleria gracilis* etc.). The southern slopes were also able to accept new thermophilous species coming from their refugies in Western and Eastern Mediterranean during the early Holocene period (e. g. *Quercus pubescens*, *Anthericum liliago*, *Gagea bohemica* etc.). Many of these thermophilous species resistant to drought form very diversified communities of grasslands and rocky grasslands. Flatter ecotopes are inhabited by hornbeam oak forest with a herbaceous layer very rich in species. The northern slopes are covered by beech forest, replaced at the bottom of canyons along the streams by an ash forest. All these features clearly delimit the district of Bohemian Karst from neighbouring districts Hřebeny and Křivoklátská pahorkatina and make it possible to relate its flora and fauna to other warm districts in Czechoslovakia (Pražská plošina, Polabí, České středohoří, South Moravia). These warm districts are united together under the name *Pannonicum* (DOSTÁL 1957) denoting a special phytogeographical region with the occurrence of thermophilous biota. A survey about flora and vegetation published SKALICKÝ and JENÍK (1974).

The development of the nature of Bohemian Karst during the Pleistocene was studied by LOŽEK (1973, 1974) on the grounds of fossil and recent *Mollusc* fauna. The development in the Holocene went through the following stages: In the preboreal period pine and birch stands were widely dispersed and the first more sensitive woody plants as oak and hazel-nut appeared. In the boreal period oak and hazel-nut predominated and other deciduous woody plants such as lime, ash, elm, maple and the majority of thermophilous shrubs appeared. Between the forests numerous open spaces occurred, where the chernosem soil was covered by steppe grassland, as may be proved by dug-up profiles containing buried chernosem with frequent remnants of the steppe mollusc *Chondrula tridens* (Müll.). In the following atlantic period the majority of the area was covered by forest, which alternated with numerous steppe enclaves on southern slopes of the hills and river valley. Human influence is marked already in the following epiatlantic period (appr. 4000 years before Christ), which meant secondary distribution of steppe formation. For the evaluation of our results it is important, that, according to Ložek's studies, the thermophilous grassland ecotopes have continuance from the last glacial period up to the present time.

BUREŠ (1970) was mapping the recent state of vegetation of the Bohemian Karst. His map gives for the Doutnáč hill these mapping units: thermophilous grassland, rocky grassland, thermophilous oak-wood (woodland), hornbeam-oak forest.

For our studies, we have chosen the thermophilous communities of grassland, rocky grassland and thermophilous oak-wood. For technical reasons we had to omit the hornbeam-oak forest. The distribution of the chosen communities on the southern slope of Doutnáč hill may be seen on Fig. 1. The less advanced succession stage is represented by the rocky grassland ecotope No. 3, next follow the grassland ecotopes No. 4 and No. 1. Here the slope is more moderate, the soil layer deeper and the plant cover denser. Thermophilous oak-wood is represented by ecotope No. 2. Detailed description of studied ecotopes and their plant cover see Chapt. 4. 1.

As far as zoological research in the Bohemian Karst is concerned, most attention was given to the fauna of different animal groups, especially to orders *Coleoptera* and *Lepidoptera* (see STREJČEK 1974). Almost no research was carried out on the communities of soil animals. The work by VERNER (1959) studying species of *Arthropoda* inhabiting the soil of oak-hornbeam forest may be cited. Interesting results were obtained by RŮŽIČKA, who studied the communities of soil animals on the rocky grassland habitat on Kotýz hill dealing with the ecology of *Diplopoda* (1968) and soil *Coleoptera* (1972). In more frequent species, the population dynamics and the vertical distribution in soil is given. These cited works as well as scattered remarks on fauna of this district have shown, that the occurrence of many thermophilous steppe and woodland species of *Arthropoda* is characteristic for Bohemian Karst.

The soils of Bohemian Karst were thoroughly studied before (MAŘAN 1947, SAMEK 1964). The soils in this limestone district were typified as rendzina (KUBIENA 1953). There occur different more or less advanced stages of rendzina types connected with the slope inclination, slope orientation towards cardinal points, with the position on the slope (foot or top of the hill), with the plant cover etc. The soils of chosen ecotopes will be described in Chapter 4.1.

3. METHODS

We have tried to obtain maximum information both about living communities and about their environment. Therefore a great number of different methods were used.

The vegetation of model sites was registered during the growing season using the method of phytocoenological records according to Braun-Blanquet. Thus the species composition and semi-quantitative estimate of different species cover was achieved. Simultaneously, a point-quadrat method was applied in the peak of the growing season in June. A cross-wire apparatus was used, described in detail in another work (KUBÍKOVÁ and REJMÁNEK 1973). About 350 point-quadrats were registered in every ecotope. For technical reasons, only the herbaceous layer in thermophilous oak-wood could be examined. Statistical evaluation of the point-quadrat method (POISSONET and POISSONET 1969) has shown that in plant communities rich in species (appr. 50 species) about 10 000 point-quadrats would be necessary to get a true picture of the cover of all species. Such work is impossible in the available time (it would last for weeks). Nevertheless, the results obtained gave valuable information about the total plant cover in different ecotopes and about the percentage frequency of dominant species. The phenology of studied communities was also noted.

From other living organisms of the ecosystem the soil microorganisms were studied. Total numbers of soil bacteria and fungi were estimated using the dilution method. For bacteria the MPA nutrient medium was used, soil fungi were cultivated on Martin's nutrient medium (peptone 5 g, glucose 10 g, $MgSO_4$ 0.5 g, agar-agar 20 g, water 1000 ml, after sterilisation 30 mg streptomycine-sulphate). The agar plates were incubated in 28 °C and colonies were counted after 3 to 5 days in bacteria, after 5 to 7 days in fungi. The suitable dilution for bacteria was 10^{-5}, for fungi 10^{-3}. The results are given in numbers in 1 g soil dry matter. The dilution method has, mainly for the estimation of soil fungi, a lot of disadvantages: for instance the just sporulating fungi are favoured in comparison with non-sporulating fungi etc. Nevertheless, it is the only method giving comparable quantitative results and as such it is widely used. For technical reasons the species composition of soil microflora could not be studied, only some remarks about dominant groups of soil *Deuteromycetes* and *Phycomycetes* were made.

Out of many other different groups of soil organisms *Tracheata* were studied by the means of quantitative soil samples and their extraction in Tullgren's apparatus. A simple cylindrical soil sampler with the base of the cylinder of 10 cm^2 and the height of 5 cm was used for taking 10 samples from every ecotope. The samples were put together in a PVC bag, taken to the laboratory and put the same day in a Tullgren apparatus. The desiccation lasted 5 days under 30 °C. Ethylalcohol (70 percent) was used as a preservative in tubes standing below. With ten samples taken from one locality, each of an area 10 cm^2, the extracted amount of *Tracheata* represented their average abundancy on 100 cm^2. In the groups *Apterygota* and *Acarina* the changes of biomass during one year were studied. To get these data the preserved animals were separated into several size classes. The biomass was then calculated using the indexes from the work by DUNGER (1968). In *Collembola* different families were differentiated, *Acarina* were divided only into *Oribatei* and other *Acarina*. In "other *Acarina*" (= *Acarina* excl. *Oribatei*) there occured mostly the two smallest size classes having nearly the same index for biomass calculation, so that the error was not magnified. Between the greater individuals of "other *Acarina*" (greater than 0.6 mm), which occured only exceptionally in the samples of described area, the members of the groups *Parasitiformes* and *Trombidiformes* were differentiated and the calculated values were added to the biomass of "other *Acarina*".

The members of *Apterygota*, *Pauropoda*, *Diplopoda* and some larvae of *Coleoptera* were determined up to the species. Most attention was paid to *Apterygota*; their taxonomical and faunistical study introduced new features for the synecological characteristics of the chosen ecotopes.

Seasonal dynamics of soil fauna was estimated by the means of five samplings during the years 1970 to 1971. Data of different samples (in the brackets the numbering of samples): 29th April 1970 (A-107, A-117, A-102, A-112), 20th July 1970 (A-108, A-118, A-103, A-113), 29th September 1970 (A-109, A-119, A-104, A-114), 10th February 1971 (A-110, A-120, A-105, A-115) and 5th April 1971 (A-111, A-121, A-106, A-116).

The faeces of soil animals were determined according to their shape, diameter and microstructure on soil slides. To be sure about the feaces of different animal groups, it was necessary to study the contents of the alimentary canal in different animal groups, their pellets in laboratory rearings, and to make direct observations in the field.

The floristical and faunistical similarity of the four chosen ecotopes was tested by Sörensen's similarity coefficient:

$$Q = \frac{2c}{a + b} \, . \, 100 \, ,$$

where a is number of the species in ecotope A, b – number of the species in ecotope B, c – number of common species in ecotopes A and B.

For the calculation of the similarity coefficient all data of presence of higher plants were used, for the similarity coefficient of *Apterygota* communities only species having an abundance at least in one sample $\geqq$ 500 ind. . m^{-2} or having constancy (in five sampling periods) Cr $\geqq$ 60 % were used.

Two tests were used to estimate the activity of soil animals and microorganisms, the one being the decomposition of cellulose, the second the output of CO_2 from the soil.

The decomposition of cellulose was estimated directly in the intact soil on the studied ecotope, using the method of TESAŘOVÁ and ÚLEHLOVÁ (1968). Leaflets of weighted filter paper (3 × 3 cm) in nylon mesh bags are put in the soil. Ten replicates in every ecotope were used. After an incubation period which in this thermophilous ecotope was 1 to 2 months, the nylon bags were taken out, the remnants of filter paper were dessicated under room temperature, carefully cleared from soil particles, dessicated to the constant weight and weighed. The loss of cellulose is given in mg . . cm^{-2} . day^{-1}.

The CO_2 output was determined according to the method of Isemeyer. The fresh sample having natural soil moisture was incubated in a closed flask above the barium hydroxide ($Ba/OH/_2$) for 24 hours under 22 °C. The rest of the barium hydroxide was titrated by chloric acid (HCl) and the amount of CO_2 produced is given in mg CO_2 . 100g soil dry matter^{-1} . 24 hours^{-1} (STEUBING 1965). The soil moisture of the samples was left unchanged to be able to get approximate data about actual soil activity in different ecotopes under their specific soil moisture conditions.

The soil itself was studied from several standpoints. Its microstructure, moisture and chemical conditions were estimated. Some measurements of soil temperature were also carried out.

The soil microstructure was studied using soil slides. The soil is sampled in an intact state in Kopecký's cylinders and dessicated under room temperature. Then it is shortly dessicated under 50 °C and embedded under vacuum in artificial resin. We have used the resin CHS 104 of Czechoslovak origin which proved most satisfactory. After several days of gradual polymerization, the samples are heated at 40 – 50 °C for several hours and then left for further polymerization under room temperature. The material may then be ground in the same manner as rock. For details see KUBÍKOVÁ (1970).

The moisture conditions of the soils were characterized by the momentary soil moisture (dessication of the samples to constant weight under 105 °C), by maximal water capacity according to Novák, by the number of hygroscopicity (in the exsicator above 10 % sulphuric acid). The momentary soil moisture is given in percent of maximal water capacity.

From the chemical constituents of the soil the main biogennic elements were studied. CaO and K_2O were estimated in the extract of 1 % citric acid by flame photometry, P_2O_5 in the extract of calcium lactate colorimetrically according to Egnér and Riehm, total nitrogen according to Kjeldahl - Foerster, total carbon according to Springer and Klee. Values of pH were estimated in water extract (1 : 2.5) and measured by pH-meter using glass and calomel electrodes.

The measurements of soil temperature were made using the summing method according to Pallmann et al. The principle of this method lays in the inversion of puffered solution of saccharose under the influence of heat. The closed tubes filled by sacharose solution are put in soil in the depth of 5 cm for appr. one month.

The soil was sampled from the upper 10 cm of the soil profile on 10 places on every ecotope and thoroughly mixed up. For microbiological and chemical estimations the fine earth was used. All estimations were done in three replicates.

4. ECOTOPES, THEIR VEGETATION AND SOIL FAUNA

4.1. DESCRIPTION OF ECOTOPES

All localities lay on the southern slope of the hill Doutnáč, with an inclination of 15° to 30° on a transect in the altitude 370 to 410 m above sea level.

Ecotope 1: 410 m above sea level, 15° inclination to South, parent rock Silurian limestones, closed xerothermic grassland, ass. *Carici-Festucetum sulcatae* KLIKA 1951. Soil subtype: Mullartige Rendzina (KUBIËNA 1953), soil profile 20 cm deep, A – C, A horizon differentiated in a thin subhorizon A_{00} (0 – 1 cm) formed by undecomposed dead mosses and plant remains, and in A_1 subhorizon of dark brown colour, densely grown through by roots of perennial grasses, with a high portion of skeleton of different categories from sand to gravel, the fine earth forming crumbs of two diameters (3 mm and 0.5 mm).

The sun radiation is not shaded and all potential direct solar irradiation is accepted here. The value of the potential direct solar irradiation depends on the latitude and on the slope inclination. The value calculated for 50° Northern lat. and for 15° slope inclination to South are 12.5 kcal . cm^{-2} . $month^{-1}$ (average for the whole year) and 17.5 kcal . cm^{-2} . $month^{-1}$ (average for growing season) – see JENÍK and REJMÁNEK (1969). The data of the microclimatic measurements published by CHOCHOLOVÁ (1960) and PACHNEROVÁ (1960) characterize the ecotope by average air temperatures, average soil temperatures, average day evaporation during a series of spring, summer and autumn measurements and average soil temperatures during one year (see Tab. 1).

Ecotope 2: 395 m above sea level, 20° inclination, parent rock Silurian limestones, stunted thermophilous oak-wood with dense shrub layer, ass. *Lathyro* (*versicoloris*)-*-Quercetum pubescentis* (KLIKA 1938) em. JAKUCS 1960. Soil subtype: Moderrendzina (MÜCKENHAUSEN 1962), soil profile 25 to 30 cm, A – C, A_{00} (0 – 2 cm) – undecomposed plant leaves and branchlets, A_{01} (2 – 10 cm) – Arthropoden Moder of dark brown colour, A_1 (10 – 25 cm) light brown Mull with earthworm pellets. Great portion of skeleton mainly in the layer of 5 to 8 cm. The sun radiation falling on the herbaceous layer is shaded by trees and shrubs, the relative light intensity alternates from 80 % in winter to 25 % in high summer (PACHNEROVÁ 1960). The values of potential direct solar irradiation for a 20° slope inclination to South are 13 kcal . . cm^{-2} . $month^{-1}$ (average for the whole year) and 18 kcal . cm^{-2} . $month^{-1}$ (average for the growing season). This radiation is accepted by the tree level, the values for

Tab. 1.

Microclimate of studied ecotopes, measured during the growing season 1959 (according to Pachnerová 1960 and Chocholová 1960)

Date		16. 4.	17. 4.	11. 6.	10. 7.	21. 8.	8. 10.	9. 10.
Air temperature (day average) in 20 cm above the ground (°C)								
Carici-Festucetum	(E-1)	20.7	19.1	13.3	33.6	23.5	15.3	15.5
Lathyro-Quercetum	(E-2)	20.8	19.3	12.5	31.3	21.9	13.9	14.3
Seseli-Festucetum	(E-3)	21.4	19.3	13.1	33.8	23.3	15.0	15.4
Soil temperature (day average) in 10 cm depth (°C)								
Carici-Festucetum	(E-1)	12.7	12.6	14.0	21.5	19.4	14.0	13.6
Lathyro-Quercetum	(E-2)	11.5	11.2	12.3	16.8	16.1	10.3	10.6
Seseli-Festucetum	(E-3)	16.4	15.8	16.2	26.5	20.2	15.7	14.9
Evaporation (day summary) in 20 cm above the ground (cm^2)								
Carici-Festucetum	(E-1)	12.3	8.3	3.6	22.4	8.7	7.9	6.1
Lathyro-Quercetum	(E-2)	12.1	7.8	2.8	24.1	8.2	5.0	4.3
Seseli-Festucetum	(E-3)	15.1	10.2	6.1	26.3	13.0	8.1	7.0

herbaceous layer are much lower as mentioned above. These conditions are reflected in soil temperatures (see Tab. 1).

Ecotope 3: 380 m above sea level, 30° inclination, parent rock Silurian limestones, opened rocky grassland, ass. *Seseli-Festucetum duriusculae* Klika 1933. Soil subtype: Protorendzina (Kubiëna 1953) only on small horizontal terraces, soil profile 2 to 5 cm, composed of coprogenic humus and skeleton. The microclimate of this locality is most extreme and highest values of air and soil temperatures and also evaporation were estimated here (Pachnerová 1960, Chocholová 1960 – see Tab. 1).The sun radiation is not shaded here. The values of potential direct solar irradiation are for 30° slope inclination to South 13.5 kcal . cm^2 . month^{-1} (average for the whole year) and 18.5 kcal . cm^{-2} . month^{-1} (average for growing season).

Ecotope 4: 375 m above sea level, 25° inclination to South, closed xerothermic grassland, ass. *Erysimo-Festucetum valesiacae* Klika 1933. Soil subtype and profile the same as Ecotope 1, sun radiation and microclimate the same as Ecotope 3.

The samples were taken from the centre of a well differentiated phytocoenosis, repeatedly from a previously delimited quadrat.

4.2. THE VEGETATION OF STUDIED ECOTOPES

The vegetation was described by the means of phytocoenological relevés and by the point-quadrat method. The results are given in Tab. 2. (relevés of grassland ecotopes), in Tab. 3 (relative frequency found by point-quadrat method in grassland ecotopes), and in Tab. 4 (relevés and point-quadrat method results for oak-wood ecotope). On the ground of comparison with the literature the communities were arranged according to the following vegetation units:

Ecotope 1: all. *Festucion valesiacae* KLIKA 1931, ass. *Carici-Festucetum sulcatae* KLIKA 1951.

Ecotope 2: all. *Eu-Quercion pubescentis* KLIKA 1957, ass. *Lathyro* (*versicoloris*) *-Quercetum pubescentis* KLIKA 1938 em. JAKUCS 1960.

Ecotope 3: all. *Alysso-Festucion pallentis* MORAVEC 1967, ass. *Seseli-Festucetum pallentis* KLIKA 1933.

Ecotope 4: all. *Festucion valesiacae* KLIKA 1931, ass. *Erysimo* (*crepidifolii*) – *Festucetum valesiacae* KLIKA 1933.

Communities on ecotope 1 and 3 are very rich in species, having 40 and 54 species respectively. Ecotope 4 is relatively poor in species due to dominancy and high vitality of *Festuca valesiaca*. The thermophilous oak-wood with its 36 species in tree and herbaceous layers may also be considered as a community rich in species.

The floristic similarity of plant communities of all 4 studied ecotopes was calculated using Sörensen's similarity coefficient. The results are as follows:

Ecotope	2	3	4
1	7.89	61.75	68.75
2		6.6	9.5
3			56.80

This survey shows clearly the greatest similarity between Ecotope 1 and 4 with plant communities belonging to the same phytocoenological alliance. High values of similarity coefficient were found also between Ecotope 3, representing dry rocky grassland, and Ecotopes 1 and 4; there are a lot of common thermophilous species in these three ecotopes. Quite different, on the contrary, is Ecotope 2, covered by thermophilous oak-wood, whose species composition is sharply different from that of the grassland ecotopes.

The results achieved by the point-quadrat method may serve for reasons explained above (Chapt. 3) only for rough orientation about percentage frequency of dominant species and about the total cover of the community. The total cover of the community

Tab. 2.

Vegetation relevés taken on grassland ecotopes

Ecotope	1	4	3
Altitude	420 m	385 m	390 m
Inclination	15°	20°	25°
Orientation	S	S	S
Total cover	100%	95%	80%
Area of rélévé	16 m^2	16 m^2	16 m^2
Date	3. 8. 1970	3. 8. 1970	3. 8. 1970
Species of the order *Festucetalia valesiacae* BR.—BL. et TX. 1943:			
Carex humilis LEYSS.	+	2.2	1.2
Koeleria gracilis PERS.	1.2	+	+
Melica transsilvanica SCHUR.	r	+	+
Helianthemum ovatum (VIV.) SCH. et THELL.	+	1.1	+
Verbascum lychnitis L.	1.3	.	1.2
Linosyris vulgaris CASS.	+	.	+
Asperula glauca (L.) BESS.	1.2	1.1	+
Calamintha acinos (L.) CLAIRV.	+	.	+
Salvia pratensis L.	+	r	+
Euphorbia cyparisias L.	r	r	+
Arabis hirsuta (L.) SCOP.	r	r	+
Thymus praecox OPIZ	1.1	+	+
Sedum boloniense (LOIS.) FENZL	+	.	1.2
Alyssum montanum L.	r	.	r
Thlaspi perfoliatum L.	+	+	1.1
Arenaria leptoclados (RCHB.) ČEL.	.	.	+
Holosteum umbellatum L.	.	.	+
Myosotis micrantha PALL.	.	.	+
Arabis auriculata LAM.	.	.	+
Valerianella olitoria (L.) PALL.	.	+	+
Veronica dillenii CR.	.	.	r
Teucrium chamaedrys L.	1.2	2.2	+
Stachys recta L.	1.1	1.1	1.1
Veronica spicata L.	1.2	+	+
Asperula cynanchica L.	2.2	.	+
Scabiosa ochroleuca L.	+	.	+
Achillea millefolium L.	+	.	.
Veronica prostrata L.	r	.	.
Medicago minima (L.) GRUFBG.	r	.	.
Scabiosa canescens W. et K.	.	.	+
Orobanche lutea BAUMG.	.	.	r
Allium montanum (SCHUR.) BECK	.	.	+
Anthericum liliago L.	.	.	r

Table 2 (continued)

Ecotope	1	4	3
Characteristic species of ass.			
Seseli-Festucetum duriusculae:			
Festuca pallens STURM.	.	.	2.2
Seseli devenyense SIMK.	.	.	2.1
Stipa capillata L.	.	.	+
Potentilla arenaria BORKH.	r	+	2.3
Pulsatilla pratensis (L.) MILL.	.	.	+
Artemisia campestris L.	.	.	1.2
Teucrium botrys L.	.	.	+
Characteristic species of ass. *Erysimo-Festucetum valesiacae* and *Carici-Festucetum sulcatae*:			
Festuca valesiaca SCHLEICH.	2.2	4.2	+
Cyanus rhenanus BOR.	+	.	+
Festuca sulcata (HACK.) NYM.	4.2	+.2	.
Accompanying species:			
Aster amellus L.	1.1	+	+
Silene nutans L.	.	.	r
Vicia hirsuta (L.) S. F. GR.	.	.	r
Vicia tetrasperma (L.) SCHREB.	2.1	2.1	.
Hypericum perforatum L.	.	.	r
Bilderdykia convolvulus (L.) DUM.	.	.	+
Erophila vulgaris DC.	.	.	+
Lithospermum arvense L.	.	.	+
Filipendula vulgaris MOENCH	.	2.1	.
Rosa canina L.	.	+	.
Thalictrum minus L.	3.2	.	.
Trifolium alpestre L.	+	+	.
Lotus corniculatus L.	1.1	.	.
Coronilla varia L.	+	.	.
Polygonatum odoratum (MILL.) DRUCE	r	.	.
Lactuca viminea (L.) PRESL	r	.	.
Cuscuta sp.	+	+	+
E_0 — Musci			
Total cover	40%	20%	50%
Thuidium abietinum	3.2	1.2	2.2
Rhytidium rugosum	1.2	+	1.2
Tortella inclinata	.	+	2.2
Toninia coeruleo-nigricans	.	r	r
Peltigera canina	.	.	r
Cladonia rangiformis	.	.	+
Grimia pulvinata	+	+	r
Orthotrichum anomalum	+	.	.
Number of species	40	28	54

Tab. 3.

Poit-quadrat analysis of grassland communities. Total number of point-quadrats 340, date 8th June 1971

Plant community	*Carici-Festucetum*		*Erysimo-Festucetum*		*Seseli-Festucetum*	
Species	Percentage frequency	Contribution of populations (in %)	Percentage frequency	Contribution of populations (in %)	Percentage frequency	Contribution of populations (in %)
Festuca valesiaca	10.41	6.28	71.9	59.98	5.9	6.34
Cyanus rhenanus	0.41	0.25	.	.	6.0	0.64
Festuca pallens	.	.	.	.	18.45	19.83
Seseli devenyense	.	.	.	.	14.49	15.59
Festuca sulcata	75.41	45.50	.	.	.	.
Carex humilis	.	.	3.96	3.30	.	.
Teucrium chamaedrys	4.16	2.51	10.06	8.39	.	.
Stachys recta	1.25	0.75	3.96	3.30	2.08	2.23
Salvia pratensis	.	.	0.41	0.34	.	.
Asperula cynanchica	8.75	5.28	.	.	.	.
Asperula glauca	.	.	5.18	4.32	1.50	1.61
Potentilla arenaria	.	.	.	.	20.20	21.72
Sedum boloniense	.	.	.	.	6.25	6.72
Koeleria gracilis	6.25	3.77	.	.	2.09	2.24
Helianthemum ovatum	.	.	4.26	3.55	1.78	1.91
Thymus serpyllum	1.25	0.75	.	.	.	.
Calamintha acinos	0.41	0.25	0.41	0.34	1.78	1.91
Aster amellus	2.08	1.25	0.42	0.34	1.50	1.61
Alyssum montanum	.	.	.	.	0.90	0.96
Hypericum perforatum	.	.	.	.	0.60	0.64
Erophila vulgaris	.	.	.	.	0.30	0.32
Thalictrum minus	37.00	22.32	.	.	.	.
Filipendula vulgaris	.	.	9.75	8.13	.	.
Vicia tetrasperma	13.33	8.04	8.23	6.86	.	.
Trifolium alpestre	.	.	0.42	0.34	.	.
Lotus corniculatus	2.08	1.25	.	.	.	.
Valerianella olitoria	.	.	0.91	0.76	.	.
Cuscuta sp.	0,41	0.25	.	.	.	.
Thuidium abietinum	.	.	.	.	10.40	11.18
Tortella inclinata	.	.	.	.	3.57	3.83
Cladonia sp.	.	.	.	.	0.60	0.64
Cerastium sp.	2.50	1.50	.	.	.	.
Sum	165.70	99.95	119.87	99.96	93.00	99.95
Point-quadrats without contact	2.08		2.74		19.00	

Tab. 4.

Record of the vegetation on Ecotope 2 — thermophilous oak-wood,
Lathyro (versicoloris)-Quercetum pubescentis (Klika 1938) Jakucs 1960

Phytocoenological relevé date 3. 8. 1970		Point-quadrat analysis of herbaceous layer. Total number of point-quadrats 340. Date 8. 6. 1971	
		Percentage frequency	Contribution of populations (in %)
E$_3$ height 6 to 8 m, cover 20%			
Fraxinus excelsior L.	30%		
Quercus pubescens Willd.	70%		
E$_{2\alpha}$ 2–3 m	80%		
Cornus mas L.	80%		
Quercus pubescens Willd.	5%		
Acer campestre L.	5%		
Crataegus monogyna Jacq.	10%		
E$_{2\beta}$ 0,5 m	10%		
Cotoneaster integerrima Med.	50%		
Ligustrum vulgare L.	20%		
Cornus mas L.	15%		
Crataegus monogyna Jacq.	15%		
E$_1$ 0.2 m	60%		
Lathyrus pannonicus (Kram.) Garcke	+		
Betonica officinalis L.	+		
Calamintha clinopodium Spenner	+		
Carex montana L.	+		
Festuca heterophylla Lam.	1.3		
Genista tinctoria L.	+		
Polygonatum odoratum (Mill.) Druce	2.2	12.57	14.96
Bupleurum falcatum L.	+		
Chrysanthemum corymbosum L.	+		
Dictamnus albus L.	1.1	8.68	10.33
Melampyrum cristatum L.	+		
Primula veris L. em. Huds.	3.3	36.82	43.83
Poa nemoralis L.	2.2	0.50	0.60
Dactylis glomerata L.	+		
Hepatica nobilis Mill.	1.2	2.69	3.20
Brachypodium pinnatum (L.) P. Beauv.	1.1	0.89	0.91
Asperula glauca (L.) Bess.	+		
Teucrium chamaedrys L.	+		
Anthericum ramosum L.	1.1		
Arabis hirsuta (L.) Scop.	+		
Origanum vulgare L.	1.1	6.28	7.48
Carex muricata ssp. *contigua* (Hoppe) Moravec	1.1		
Galium aparine L.	1.2	9.28	11.05
Bilderdykia convolvulus (L.) Dum.	+		

Table 4 (continued)

Phytocoenological relevé date 3. 8. 1970		Point-quadrat analysis of herbaceous layer. Total number of point-quadrats 340. Date 8. 6. 1971	
		Percentage frequency	Contribution of populatioos (in %)
Sedum telephium L.	+		
Alliaria officinalis ANDRZ.	1.1	2.69	3.20
Campanula persicifolia L.	+		
Lactuca quecina L.	+	3.59	4.27
Silene nutans L.	r		
Number of species	36	Sum 83.99	99.82
Number of species of herbaceous layer	29	10	

may be calculated from the percentage of point-quadrats without a hit. This is 2, 19 and 3 percent in Ecotopes 1, 3 and 4 respectively, thus showing clearly the open character of the vegetation on rocky grassland (Ecotope 3) in comparison to the closed tussocks of grassland ecotopes No. 1 and 4. The differences in percentage cover of various species on the three compared grassland ecotopes are very markedly seen on the dominant species of the genus *Festuca* (see Fig. 3). The dominant growth of *Festuca sulcata* on Ecotope 1 is a sign of less extreme microclimatic conditions on

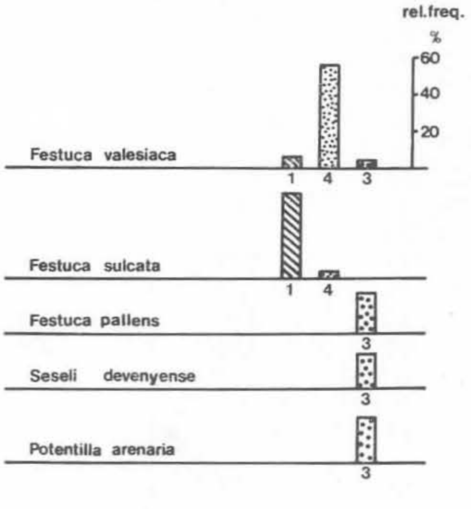

Fig. 3. Relative frequency of dominant species on grassland ecotopes No. 1, 3, 4 reflecting the ecological differences of the stands.

this ecotope manifested in higher moisture and soil depth. *Festuca valesiaca* is able to sustain more extreme conditions being further exchanged by *Festuca pallens* on rocky ecotope. PUČELÍKOVÁ (1967) in her comparative ecological study on these *Festuca* species found higher occurence of *Festuca valesiaca* on ecotopes with shallow soil, with slope inclination 20 to 30°. *Festuca sulcata* is less resistant to desiccation, but it has much greater competitive ability on mesophilous ecotopes thus eliminating the occurence of *Festuca valesiaca*.

Tab. 5.

Ecotope 1 (*Carici-Festucetum*) — abundance of all animal groups estimated on 100 cm^2

	1970			1971	
	April	July	Sept.	Febr.	April
	(A-107)	(A-108)	(A-109)	(A-110)	(A-111)
Mesofauna:					
Apterygota	103	227	85	249	271
Oribatei	964	869	784	448	629
"other *Acarina*"	381	239	223	113	144
Pauropoda	3	2	1	5	2
Coccinea	—	1	1	5	—
Thysanoptera	—	2	2	3	1
Nematoda	1	12	—	3	2
Macrofauna:					
Enchytraeidae	18	12	—	32	9
Pseudoscorpionidae	1	1	2	—	1
Arachnida	2	1	—	—	—
Symphyla	1	—	—	—	—
Diplopoda	8	5	11	—	—
Chilopoda	—	—	—	—	1
Coleoptera:					
Staphylinidae	4i*	—	1i	—	—
Curculionidae	1l**	—	—	—	—
Pedinus sp.	1l	2l	5l	—	—
Chrysomelidae	1l	—	—	—	—
Diptera	1i	1i6l	4l	9l	2l
Heteroptera	—	1l	—	—	—
Auchenorrhyncha	6l	—	1l	—	2l
Lepidoptera	1l	1l	1l	—	—
Hymenoptera	—	—	1i	—	3i

*i — imago, **l — larva.

4.3. SOIL MESO- AND MACROFAUNA OF STUDIED ECOTOPES

The soil animals as well as plants react very precisely on the influence of microclima, of soil conditions, of the presence of other biota forming communities characterizing the different ecotopes. These communities can be therefore very suitably used for the differentiation of ecosystems.

The Tab. 5–8 give numbers of individuals of main groups of soil animals, found in different samples; numbers denote the abundance of animals on 100 cm^2. The

Tab. 6.

Ecotope 2 (*Lathyro-Quercetum*) — abundance of all animal groups estimated on 100 cm^2

	1970			1971	
	April	July	Sept.	Febr.	April
	(A-117)	(A-118)	(A-119)	(A-120)	(A-121)
Mesofauna:					
Apterygota	239	146	61	145	264
Oribatei	984	473	578	722	893
"other *Acarina*"	154	95	133	86	127
Pauropoda	1	—	—	—	—
Coccinea	2	—	—	—	—
Thysanoptera	1	—	1	—	—
Macrofauna:					
Enchytraeidae	6	1	—	—	2
Pseudoscorpionidae	2	1	1	1	—
Arachnida	2	—	1	1	3
Symphyla	4	3	—	—	1
Diplopoda	10	3	4	3	5
Chilopoda	4	1	—	—	1
Coleoptera:					
Carabidae	—	—	—	—	1i
Staphylinidae	1i	—	—	—	—
Curculionidae	—	1l	—	—	—
other *Coleoptera*	—	—	—	3l	2i
Diptera	7l	1l	5l	6l	9l
Hymenoptera	3i	4i	6i	1i	1i
Raphidia sp.	—	—	—	1l	1l
Lepidoptera	—	—	1l	1l	—

method of soil sample desiccation in Tullgren's apparatus is sufficiently effective for *Arthropoda*. For the quantitative extraction of *Nematoda* and *Enchytraeidae* from soil samples other methods are being used, nevertheless it is possible to judge from the obtained numbers of animals on greater or smaller populations of these groups occurring on different ecotopes and on their share in soil development. *Isopoda*, who play significant role in soil development, were not obtained by sample desiccation, but collected under stones and gravel on Ecotope 2.

Tab. 7.

Ecotope 3 (*Seseli-Festucetum*) — abundance of all animal groups estimated on 100 cm^2

	1970			1971	
	April	July	Sept.	Febr.	April
	(A-102)	(A-103)	(A-104)	(A-105)	(A-106)
Mesofauna:					
Apterygota	49	86	14	110	72
Oribatei	181	360	184	222	292
"other *Acarina*"	176	78	90	153	125
Pauropoda	—	—	—	1	—
Coccinea	1	1	2	2	—
Thysanoptera	—	—	1	1	—
Psocoptera	—	1	—	—	—
Nematoda	4	—	—	—	—
Macrofauna:					
Enchytraeidae	6	4	—	17	—
Arachnida	—	—	1	4	4
Diplopoda	—	1	—	—	4
Coleoptera:					
Carabidae	—	—	—	—	1l
Staphylinidae	—	—	1i	—	2i
Pedinus sp.	1l	—	1l	1l	—
Curculionidae	—	—	—	1i	—
Lamellicornia	—	—	—	—	1l
other *Coleoptera*	—	—	—	2l	—
Diptera	2l	6l	1i	1l	—
Heteroptera	2l	1i	2l	—	—
Lepidoptera	1l	—	—	—	—

Tab. 8.

Ecotope 4 (*Erysimo-Festucetum*) — abundance of all animal groups estimated on 100 cm^2

	1970			1971	
	April	July	Sept.	Febr.	April
	(A-112)	(A-113)	(A-114)	(A-115)	(A-116)
Mesofauna:					
Apterygota	153	35	48	194	430
Oribatei	634	247	502	705	533
"other *Acarina*"	296	72	191	141	185
Pauropoda	1	—	2	—	—
Coccinea	16	3	15	19	7
Thysanoptera	—	—	22	6	2
Nematoda	2	9	—	—	2
Macrofauna:					
Enchytraeidae	16	4	—	16	7
Pseudoscorpionidae	3	—	2	1	—
Arachnida	—	—	1	—	2
Diplopoda	9	2	3	—	6
Coleoptera:					
Staphylinidae	1i	—	—	1i	—
Prinomus melanarius	—	11	—	—	11
Pedinus sp.	—	—	11	—	—
Curculionidae	—	—	1i	1i	—
Halticidae	—	—	—	1i	—
other *Coleoptera*	—	—	—	21	—
Diptera	51	2i	11	21	41
Auchenorrhyncha	—	—	—	—	1i
Lepidoptera	—	—	—	21	11
Hymenoptera	—	—	18i	3i	16i

4.3.1. Soil animal populations on grassland ecotopes (No. 1 and 4)

Ecotopes 1 and 4, covered by grassland of *Festucion valesiacae*, are similar in many features and therefore they are evaluated here together.

Both ecotopes are characterized by the presence of *Diplopoda* represented by *Leptophylum nanum* LATZEL, 1884 and *Chromatojulus unilineatus* KOCH, 1838. The abundance of *Diplopoda* here is 900 to 1100 individuals . m^{-2}. Also *Enchytraeidae* play a significant role here during the whole year excluding the dry period at the end of summer and at the beginning of autumn. *Diptera* larvae are also relatively abundant here, but the estimated species do not play a very important role in soil development, belonging for the most part to the group *Brachycera* with sucking mouthparts. The drier ecotope 4 is inhabited by a greater number of *Formicidae*. Other groups of soil macrofauna are not important from the view-point of soil development, being carnivorous or herbivorous (not saprozoic).

The soil mesofauna is represented on both ecotopes by a high number of individuals of *Acarina* and *Apterygota*. As mentioned above, *Acarina* in this work are divided into *Oribatei* and "other *Acarina*". From the view-point of soil development only *Oribatei* must be taken into account, "other *Acarina*" are mostly predaceous or phytophagous. The maximal abundance on Ecotope 1 was for *Oribatei* 96 400 individuals . m^{-2}, for "other *Acarina*" 38 100 individuals . m^{-2}; on drier ecotope 4 the estimated maximal abundance of *Oribatei* was 70 500 individuals . m^{-2}, of "other *Acarina*" only 29 600 individuals . m^{-2}.

The numbers of *Apterygota* are lower: on more humid Ecotope 1 their abundance reaches 27 100 ind. on m^{-2}, on drier Ecotope 4 it is 43000 ind. m^{-2}.

From other groups of soil mesofauna, members of euedafobiont *Pauropoda*, very sensitive to soil desiccation, occur regularly on Ecotope 1. They are represented here by *Allopauropus tripartitus* KRESTEWA, 1940 (7 ind.), *Allopauropus gracilis* var. *sabaudianus* REMY, 1930 (4 ind.) and *Allopauropus cuenoti* REMY, 1931 (4 ind.). Furthermore, Ecotope 4 is characterized by phytophagous *Coccinea*.

Apterygota from all ecotopes were determined up to the species. This enabled precise delimitation of *Apterygota* communities, their interrelations and general characteristics of the studied ecosystems. Tab. 9 gives all species of *Apterygota* found on all ecotopes studied.

Ecotope 1 (*Carici-Festucetum*) is characterized by this species combination (arranged according to decreasing dominancy and constancy): *Cryptopygus bipunctatus* – *Onychiurus armatus* – *Sphaeridia* sp. – *Isotomodes productus* – *Isotoma notabilis* – *Metaphorura bipartita* – *Doutnacia xerophila* – *Mesaphorura krausbaueri* – *Eosentomon transitorium* – *Sminthurinus aureus* – *Lepidocyrtus lanuginosus* – *Isotomiella minor*.

Ecotope 4 (*Erysimo-Festucetum*) is characterized by following species combination: *Isotoma notabilis* – *Onychiurus armatus* – *Xenylla boerneri* – *Isotomodes sexsetosus* – *Sphaeridia* sp. – *Mesaphorura krausbaueri* – *Isotomodes productus* – *Metaphorura bipartita* – *Isotomiella minor* – *Isotomodes armatus* – *Mesaphorura tenuisensilata* – *Proturentomon* sp. – *Entomobrya* sp. – *Doutnacia xerophila*.

4.3.2. Soil animal populations on woodland ecotope (*Lathyro-Quercetum*)

The soil under thermophilous oak-wood is inhabited regularly by *Diplopoda* *Chromatojulus unilineatus* and *Leptophylum nanum* and larvae of *Diptera*. The larvae of *Diptera* belong mostly to the families *Bibionidae* and *Tipulidae* and contribute to

Tab. 9.

Abundance of all Apterygota species estimated on studied area (on 100 cm^2)

Ecotope (No.)	3					1					4					2				
Plant community	*Seseli - Festucetum*					*Carici - Festucetum*					*Erysimo - Festucetum*					*Lathyro - Quercetum*				
Sample (No.)	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121
Onychiurus armatus (Tullb.) s. Stach, 1954	11	3	—	28	16	15	70	12	31	35	13	8	8	46	70	3	3	4	3	10
Metaphorura affinis (Börner, 1902)	—	3	—	—	7	3	1	7	—	12	—	—	11	4	9	36	5	1	2	—
Entomobrya cf. *handschini* Stach, 1922	1	3	1	7	15	—	—	9	—	6	1	—	6	2	—	6	5	2	1	9
Mesaphorura krausbaueri (Börner) s. Rusek, 1971	5	1	—	—	2	2	—	5	9	3	9	—	—	22	10	—	—	—	—	—
Isotomodes productus (Axelson) s. da Gama, 1963	2	2	—	—	10	10	20	5	—	25	12	3	—	1	11	—	—	—	—	—
Xenylla boerneri Axelson, 1905	26	28	4	36	10	—	—	—	—	—	—	3	8	20	86	3	—	—	—	—
Eosentomon mixtum Condé, 1945	1	—	—	18	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Isotoma notabilis Schäffer, 1896	—	—	2	—	—	1	3	1	9	37	5	7	3	63	91	25	46	2	32	37
Isotomiella minor (Schäffer, 1896)	—	—	1	—	—	1	—	2	1	1	1	—	—	9	11	22	22	10	10	21
Lepidocyrtus lanuginosus (Gmelin) s. Gisin, 1964	—	—	—	—	—	—	2	4	—	1	—	—	6	—	5	—	—	9	—	1
Isotomodes sexsetosus da Gama, 1963	—	—	—	—	—	—	—	—	—	—	53	—	7	1	31	—	—	—	—	—
Mesaphorura tenuisensillata Rusek, 1974	—	—	—	—	—	—	—	—	—	—	13	1	1	—	—	8	—	—	—	—
Isotomodes armatus Naglitsch, 1962	—	—	—	—	—	—	—	—	—	—	3	2	1	1	10	—	—	—	—	—
Proturentomon sp.	—	—	—	1	—	—	—	—	—	—	3	—	2	2	3	1	3	—	2	—

Cryptopygus bipunctatus (Axelson, 1903)	—	—	—	12	1	48	57	20	171	113	—	—	1	—	—	35	18	—	7	17
Eosentomon transitorium Berlese, 1908	—	—	—	—	—	4	2	1	3	2	—	—	—	4	1	4	—	2	6	7
Sminthurinus aureus (Lubbock, 1862)	—	—	—	—	—	4	—	1	5	2	1	—	—	—	1	—	—	—	—	—
Doutnacia xerophila Rusek, 1974	—	—	—	—	—	6	5	3	8	4	1	—	1	2	2	—	1	1	3	—
Folsomia quadrioculata (Tullberg, 1871)	—	—	—	1	—	—	—	3	—	—	—	—	—	—	—	37	14	15	45	146
Lepidocyrtus lignorum (Fabricius) s. Gisin, 1964	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	8	12	1	—	1
Eosentomon bohemicum Rusek, 1966	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	8	6
Metaphorura sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	9	5	—
Mesaphorura sylvatica (Rusek, 1971)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	6	3
Sphaeridia sp.	2	—	—	—	—	25	62	—	2	24	21	5	—	3	9	1	—	—	—	—
Sminthurus sp. juv.	1	44	—	—	—	1	—	—	—	1	11	—	—	1	2	10	—	—	—	—
Hypogastrura socialis (Uzel, 1891)	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Onychiurus pseudogranulosus Gisin, 1951	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Onychiurus denisi Stach, 1934	—	—	2	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—
Pseudosinella decipiens Denis, 1924	—	—	1	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pseudosinella ksenemani Gisin, 1944	—	—	1	—	—	—	—	1	—	—	—	—	1	—	—	—	5	1	—	—
Ceratophysella sp.	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mesaphorura sp.	—	—	—	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Isotoma cf. *viridis* Bourlet, 1839	—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Micranurida sp.	—	—	—	—	2	—	2	—	4	2	—	—	—	—	1	2	1	—	—	—

Tab. 9 (continued)

Ecotope (No.)	3					1					4					2				
Plant community	*Seseli - Festucetum*					*Carici - Festucetum*					*Erysimo-Festucetum*					*Lathyro - Quercetum*				
Sample (No.)	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121
Willemia anophthalma BÖRNER s. HÜTHER, 1962	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Deuterosminthurus sp. juv.	—	—	—	—		1	1	—	—	1	—	—	—	—	—	—	—	—	—	—
Sminthurus maculatus TÖMÖSVARY, 1883	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Megalothorax minimus WILLEM, 1900	—	—	—	—	—	—	1	—	—	—	—	—	—	3	2	2	—	—	—	2
Pseudachorutes parvulus BÖRNER, 1901	—	—	—	—	—	—	—	2	2	2	—	—	1	—	—	—	—	—	12	1
Friesea mirabilis (TULLBERG, 1871)	—	—	—	—	—	—	—	2	—	—	—	—	—	2	1	—	—	—	—	2
Lepidocyrtus paradoxus UZEL, 1890	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Seira sp.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Orchesella multifasciata STSCHERBAKOW, 1898	—	—	—	—	—	—	—	1	1	—	—	1	—	—	—	—	1	—	—	—
Lepidocyrtus sp.	—	—	—	—	—	—	—	—	—	—	2	2	—	1	—	—	—	—	—	—
Karlstejnia annae RUSEK, 1974	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Arrhopalites sp.	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—
Hypogastrura sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Sminthurinus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—
Eosentomon delicatum GISIN, 1945	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Isotoma sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—

Cyphoderus albinus NICOLET, 1841	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Eosentomon germanicum PRELL, 1912	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Acerentomon tuxeni NOSEK, 1961	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—
Onychiurus absoloni (BÖRNER, 1901)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Willemia aspinata STACH s. HÜTHER, 1962	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Lathriopyga conjuncta (STACH, 1926)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—

the formation of structural soil particles. *Enchytraeidae* were found considerably less than on grassland ecotopes. Some members of *Isopoda* were found by individual sampling.

Soil mesofauna is represented here by *Oribatei* with maximal abundance 98 400 ind. m^{-2}, by "other *Acarina*" with abundance 15 400 ind. m^{-2}, and *Apterygota* with maximal abundance 26 400 ind. m^{-2}.

The *Apterygota* community is characterized by the following species combination: *Folsomia quadrioculata* – *Isotoma notabilis* – *Isotomiella minor* – *Cryptopygus bipunctatus* – *Metaphorura bipartita* – *Onychiurus armatus* – *Entomobrya* sp. – *Metaphorura* sp. – *Lepidocyrtus lignorum* – *Eosentomon transitorium* – *Eosentomon bohemicum* – *Mesaphorura sylvatica* – *Proturentomon* sp. – *Doutnacia xerophila*.

Out of these species *Isotoma notabilis*, *Isotomiella minor*, *Metaphorura bipartita*, *Onychiurus armatus*, *Doutnacia xerophila* are common to grassland and woodland ecotopes; two more species are common to woodland and more mesic grassland with dominant *Festuca sulcata*, e. g. *Cryptopygus bipunctatus* and *Eosentomon transitorium*, leaving thus *Folsomia quadrioculata*, *Metaphorura* sp., *Lepidocyrtus lignorum*, *Eosentomon bohemicum* and *Mesaphorura sylvatica* as true woodland soil animals.

4.3.3. Soil animal populations on rocky grassland ecotope 3 (*Seseli-Festucetum*)

The communities on rocky grassland ecotope represent the least advanced stage of a successional series of xerothermic grassland ecosystems of the hill Doutnáč. This ecotope is characterized by irregularities in the occurrence of edaphobionts during the year, due to alternating moisture and temperature conditions. Some groups of soil macrofauna occur here only in the spring and in the winter under suitable soil moisture conditions. The abundance of macrofauna is very low. The soil formation is influenced mainly by soil mesofauna. The maximal abundance of *Oribatei* is here 36 000 ind. m^{-2}, of "other *Acarina*" 17 600 ind. m^{-2}, of *Apterygota* 11 000 ind. m^{-2}.

The community of *Apterygota* is represented here by the species combination of five species only: *Xenylla boerneri* – *Onychiurus armatus* – *Entomobrya* sp. – *Mesaphorura krausbaueri* – *Isotomodes productus*.

Out of these *Onychiurus armatus* is present in all four thermophilous communities on the southern slope of Doutnáč hill, *Isotomodes productus* and *Mesaphorura krausbaueri* is common to this rocky grassland ecotope and both grassland ecotopes, *Xenylla boerneri* and *Entomobrya* sp. are common to rocky grassland, and to dry grassland with dominant *Festuca valesiaca*. There is no species which would be present only in this most extreme ecotope. Thus *Apterygota* communities here are differentiated only by negative features, by the absence of a group of more sensitive species, not by the presence of specialized characteristic species.

4.3.4. Coenological relations of *Apterygota* communities

Coenological relations and faunistic similarity of studied ecotopes were estimated using the Sörensen's similarity coefficient. Only characteristic species were used for calculations (A $\geqq$ 500 ind. m^{-2} and Cr $\geqq$ 60%).

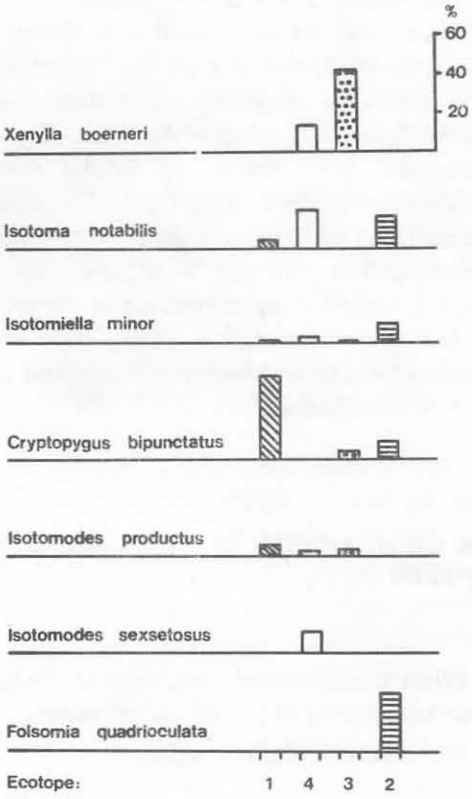

Fig. 4. Relative frequency of dominant Apterygota species on the ecotopes studied.

The calculated values are given in following survey:

Ecotope	2	3	4
1	58.8	48.0	57.1
2		40.0	53.6
3			50.0

The values show the sequence of similarity of estimated communities. Least similar are communities living in woodland soil and rocky grassland soil (Ecotopes 2 and 3), which corresponds to the ecological and floristical diversity of these ecotopes. The sequence from less similar to more similar communities proceeds in following manner: rocky grassland – mesic grassland, rocky grassland – thermophilous grassland, woodland – thermophilous grassland, thermophilous grassland – mesic grassland, woodland – mesic grassland.

These coenological relations of *Apterygota* communities are very interesting in comparison with Sörensen's similarity coefficient of plant cover. These results will be discussed in following chapter.

Fig. 4 shows different dominance of some characteristic species common for several ecotopes, which may be used as a further differentiating feature. *Isotomodes productus* is common for all grasslands, *Xenylla boerneri* is characteristic for dry grasslands (*Seseli-Festucetum duriusculae* and *Erysimo-Festucetum valesiacae*). *Isotomodes sexsetosus* is a highly specialized species occuring only in the soil type Mullartige Rendzina under *Carici-Festucetum sulcatae*. *Doutnacia xerophila* is typical for ecotopes with differentiated soil profile, it is missing in undeveloped soil of rocky grassland. The same may be said about *Isotoma notabilis*. On the other hand *Folsomia quadrioculata* is a typical woodland species, missing in the grasslands.

Apterygota communities of the same or very similar composition were found in Czechoslovakia in Moravian Karst and on Pavlovské vrchy (South Moravia) – Rusek, unpublished.

4.4. COMPARISON OF THE COENOSES OF HIGHER PLANTS AND APTERYGOTA

When the Sörensen's similarity coefficient was calculated both for higher plants and Apterygota, very marked differences in the resulting values could be seen.

Sörensen's similarity coefficient:

	Higher plants			*Apterygota*		
Ecotope	2	3	4	2	3	4
1	7.9	61.7	68.7	58.8	48.0	57.1
2		6.6	9.5		40.0	53.6
3			56.8			50.0

In the botanical material, the woodland (No. 2) is sharply differentiated from grasslands (Nos. 1, 3, 4), the similarity coefficients being only 7.9; 6.6; 9.5 respectively. Only 3 species are common to grasslands and woodland, e. g. *Asperula glauca*, *Teucrium chamaedrys*, *Arabis hirsuta*, out of the whole numbers of 76, 90 and 63 species. On the contrary, there is high floristical similarity between all three grasslands, the highest of them all is between the two closed grasslands of the *Festucion valesiacae*, with slight differentiation towards the *Seseli-Festucetum duriusculae* (Ecotope No. 3).

A quite different picture is presented by the analysis of *Apterygota* communities. The similarity coefficients are relatively high for all ecotopes. There is no sharp differentiation between grasslands and woodland. On the contrary, nearly the same value was calculated for relations between woodland and grasslands (2 – 1, 2 – 4) and between both grasslands (1 – 4). On the other hand, there is a marked differentiation of the rocky grassland No. 3, having somewhat lower coefficient with all the other ecotopes, with marked decrease of the value woodland – rocky grassland.

These results show, how homogeneous conditions in the soil influence the species composition. There exists a number of ubiquitous species of soil animals with great ecological amplitude. In higher plants, the ecological amplitude is much more narrow and they react very quickly to changes in light, moisture, and nutrients. Thus the developmental changes and the oscilations on the border between xerothermic grassland and woodland are markedly seen on the higher plant cover of the locality. The populations of *Apterygota* are much more conservative and "momentary" changes in climate and plant cover have not such immediate effect.

This feature of soil animal populations may be used in solving the much discussed question of continuity of continental steppe formation in our country. The model site analysis shows that according to *Apterygota* populations the grassland ecotope No. 1, *Carici-Festucetum*, must have been for a certain time under woody plant cover, because it still holds a number of species common with the woodland. On the contrary, no woodland species were found on rocky grassland ecotope No. 3, *Seseli-Festucetum*, thus enabling us to suppose that no forest cover has ever been present here.

Similar conclusions may be drawn from analysis of soil fungi population (see FASSATIOVÁ 1966) thus pointing to the importance of complex coenological study.

5. DYNAMICS OF ENVIRONMENTAL AND BIOTIC FACTORS

Environmental factors and biota of the chosen ecotopes were studied at approximately two-month intervals. Pronounced fluctuations could be registered during repeated samplings. The results for single environmental factors and biota are shown in Figs. 5 to 8 and 11 to 16 and discussed in detail in the following chapters.

5.1. ENVIRONMENTAL FACTORS

5.1.1. Soil moisture

The results of momentary soil moisture given in percent of maximal capillar water capacity are presented in Tab. 10 and Fig. 5. Tab. 11 gives the maximal capillar water capacity and hygroscopic water for the studied soils.

The values on rocky grassland, *Seseli-Festucetum* (Ecotope 3) are markedly

Tab. 10.

The dynamics of soil moisture in percent maximal capillar water capacity on investigated ecotopes during the period studied (1970—1971)

Date	29. 4.	10. 5.	9. 6.	20. 7.	3. 8.	8. 9.	29. 9.	10. 11.	3. 2.	5. 4.	Year average
Carici-Festucetum (E-1)	57.7	46.7	46.2	34.3	43.0	17.5	21.9	49.4	59.8	57.3	43.4
Lathyro-Quercetum (E-2)	73.2	37.1	59.7	23.0	48.6	31.3	22.9	45.2	80.0	81.4	50.2
Seseli-Festucetum (E-3)	106.1	59.2	75.1	60.5	109.3	21.3	9.7	85.6	139.3	81.4	74.7
Erysimo-Festucetum (E-4)	59.7	42.8	44.2	33.6	38.5	22.1	14.1	44.8	48.0	52.4	40.1

Tab. 11.

ECOTOPE	Maximal capillar water capacity		Hygroscopic water	
	g. 100 cm^{-3}	g. 100 g dry matter^{-1}	g. 100 g dry matter^{-1}	% max. capillar water capacity
Carici-Festucetum (E-1)	70.3	149.5	11.5	7.69
Lathyro-Quercetum (E-2)	56.7	115.1	10.2	8.86
Seseli-Festucetum (E-3)	54.4	80.2	9.9	12.34
Erysimo-Festucetum (E-4)	69.0	143.1	11.2	7.82

different from the values characteristic for grasslands and thermophilous oak-wood. The fluctuations in momentary soil moisture are the greatest here, which relates to shallow soil, opened vegetation cover and slope inclination. Also the maximal capillar capacity is the lowest here in dependance to the type of soil microstructure (see Chapter 6). Nevertheless, the water supply was sufficient for the majority of the studied period, the values being mostly higher than 60 % maximal capillar water capacity. However, in dry periods the soil gets desiccated up to the number of hygroscopicity, in moist periods, on the contrary, it gets water-logged (see the value for February).

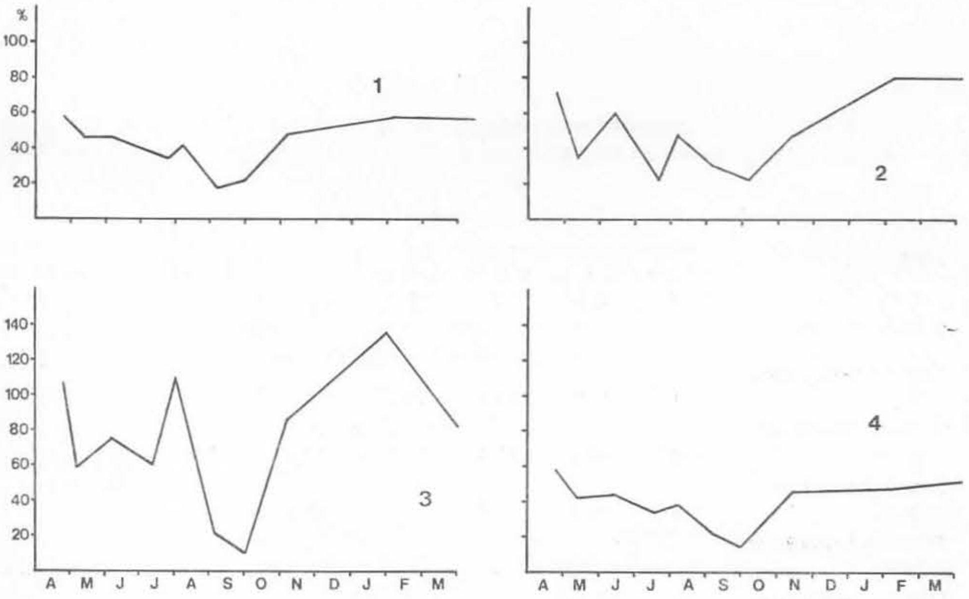

Fig. 5. Dynamics of actual soil moisture (in percent of maximal capillar water capacity) during the period studied.

The moisture conditions of both grasslands, *Carici-Festucetum* and *Erysimo-Festucetum*, (Ecotope 1 and 4) are much more constant during the whole year. With high maximal water capacity of Mullartige Rendzina soil subtype of these ecotopes, their momentary soil moisture is rather low, mostly not reaching 60 % of maximal water capacity. However, they never become desiccated or water-logged.

Somewhat higher values than on grasslands were found in the woodland, *Lathyro-Quercetum*, (Ecotope 2), where the soil surface is shaded and direct evaporation from the soil is diminished. On the other hand, the output of water is higher in the structurally more complicated stand. The values estimated show marked decrease in soil moisture in the spring and summer during the intensive growth of roots and branches of woody-plants.

The dynamics of momentary soil moisture was estimated in the work of Chocholová (1960) in the years 1958 to 1959 on similar ecotopes with similar results.

5.1.2. Soil temperature

Soil temperature depends on potential direct solar irradiation, on soil features like microstructure, humus content, moisture, on parent rock composition, and on plant cover. Daily and seasonal fluctuations of temperature are influenced by the same factors.

Highest temperatures and also the greatest range of temperature fluctuations were found on rocky grassland with open plant cover. The slope orientation and

Tab. 12.

Average soil temperature (measured according to Pallmann method in 5 cm depth) during the growing season 1959 (according to Pachnerová 1960) and during the growing season 1970

Date	1959						1970	
	29. 1. to 25. 4.	25. 4. to 4. 6.	4. 6. to 2. 7.	2. 7. to 25. 7.	25. 7. to 14. 8.	18. 9. to 6. 1.	20. 7. to 3. 8.	29. 9. to 10. 11.
Carici-Festucetum (E-1)	7.9	10.5	14.7	15.7	17.9	9.1	22.5	9.9
Lathyro-Quercetum (E-2)	5.8	10.3	11.4	12.7	16.5	7.4	20.1	9.5
Seseli-Festucetum (E-3)	6.4	14.8	17.5	18.2	19.8	10.4	26.7	10.2
Erysimo-Festucetum (E-4)	—	—	—	—	—	—	23.4	10.2
Day average temperature on the climatic station in Beroun	—	—	—	—	—	—	20.5	10.3

inclination influence the optimal values of potential direct sun radiation which is excepted freely by sparsely covered shallow soil. On the other hand, the loss of warmth at night and in winter is much quicker and the temperatures fall more than in the grasslands. In February, for example, at one sampling period, the soil profile on rocky grassland was deep frozen, contrary to soil profile under grassland, which was completely melted.

The grasslands (Ecotope 1 and 4) have more constant conditions of soil temperature than rocky grassland. The maximal temperatures are lower, but also the range of fluctuations is smaller.

The soil temperatures in oak-wood were relatively lowest, due to dense cover of trees and shrubs.

The values measured by PACHNEROVÁ (1960) together with our own measurements see in Tab. 12.

5.1.3. The values of pH

The estimated values of pH are given in Tab. 13.

The values of pH are nearly the same on different ecotopes, only there is a weak tendency to the increase of pH on the rocky grassland, where the shallow layer of Protorendzina is in contact with limestone skeleton, which continuously enriches the soil with cations.

Tab. 13.

Values of pH (H_2O) estimated on investigated ecotopes

Date		29. 4.	20. 7.	29. 9.	10. 11.	3. 2. 1971	year average
Carici-Festucetum	(E-1)	7.09	7.12	7.12	7.30	7.60	7.24
Lathyro-Quercetum	(E-2)	7.12	7.30	7.30	7.40	7.70	7.38
Seseli-Festucetum	(E-3)	7.30	7.29	7.45	7.40	7.80	7.44
Erysimo-Festucetum	(E-4)	7.20	7.18	7.22	7.35	7.65	7.32

During the winter the values of pH increased on all ecotopes appr. of 0.5° pH. The same increase was observed in the content of Ca ions in the soil. This suggests that in winter the weathering of soil skeleton is intensified due to temperatures alternating around the freezing point.

Similar values of pH on limestone rocks were found by KUČEROVÁ (1960) on Doutnáč hill and KUBÍKOVÁ (1971) on Velká hora hill.

5.1.4. Content of Ca ions in the soil

The values estimated are given in Tab. 14 and Fig. 6.

Relatively the highest values were found in the rocky grassland (compare the values of pH). The content of Ca ions is constant in all the ecotopes during the growing period, but suddenly in the winter the twofold increase occured. This may be explained by more intensive weathering and by the absence of uptake by the plant roots.

The estimated values lay in the range of 0.25 to 1.1 %. Similar values were found by Sobotka, Langkramer and Kholová (1967) on grassland and woodland localities in Bohemian Karst. Kovacs-Láng (1966) in her work on xerothermic vegetation in northern Hungary found the Ca ion content about 2 % on limestone and 1.7 % on dolomite. Úlehlová (1964) compared the soils of 40 different stands of *Stipa* spec. div. and found the range of Ca ion content from 0.1 to 1.1 %. The content of Ca ions in the soils of xerothermic communities on South Moravia on limestone parent rock (Moravský kras, Pavlovské vrchy) was in the range of 0.5 to 1 %, similarly on south and western slopes of the basalt hill Oblík in České středohoří. The content of Ca ions in the soil of xerothermic communities on different parent rocks in the suburb of Prague was 0.2 to 1.5 % (Kubíková, in lit.). Kolbek (1973) gives for grassland and

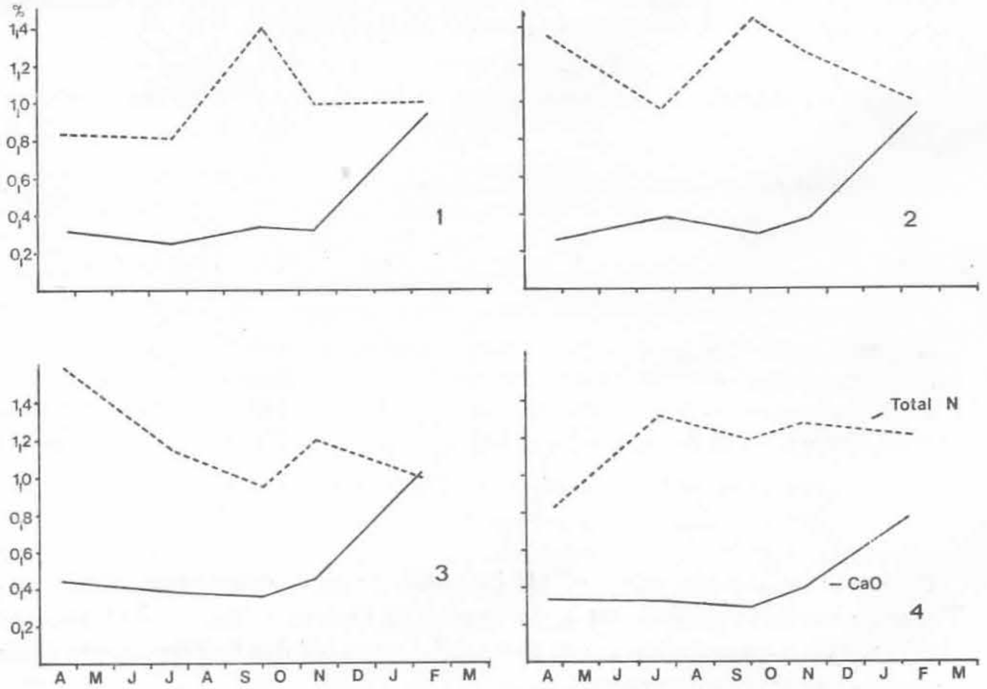

Fig. 6. Dynamics of total nitrogen content (dashed line) and CaO content (full line) during the period studied.

Tab. 14.

Values of CaO (in % soil dry matter) estimated on investigated ecotopes

Date		29. 4.	20. 7.	29. 9.	10. 11.	3. 2. 1975	year average
Carici-Festucetum	(E-1)	0.317	0.245	0.332	0.317	0.812	0.405
Lathyro-Quercetum	(E-2)	0.267	0.385	0.295	0.385	0.937	0.454
Seseli-Festucetum	(E-3)	0.450	0.392	0.355	0.450	1.085	0.546
Erysimo-Festucetum	(E-4)	0.332	0.317	0.295	0.392	0.787	0.425

rocky grassland communities in České středohoří following results in the range of 0.32–2.1 %.

All these results show relatively very high content of Ca ions in these subtypes of Rendzina soils. The highest values were found in the least advanced stages of the soil.

5.1.5. Content of K ions in the soil

The results are given in Tab. 15 and Fig. 7.

The estimated values of K ion content were in the range of 9 to 20 mg/100 g on grassland and rocky grassland ecotopes; in the woodland they lay much higher, in the

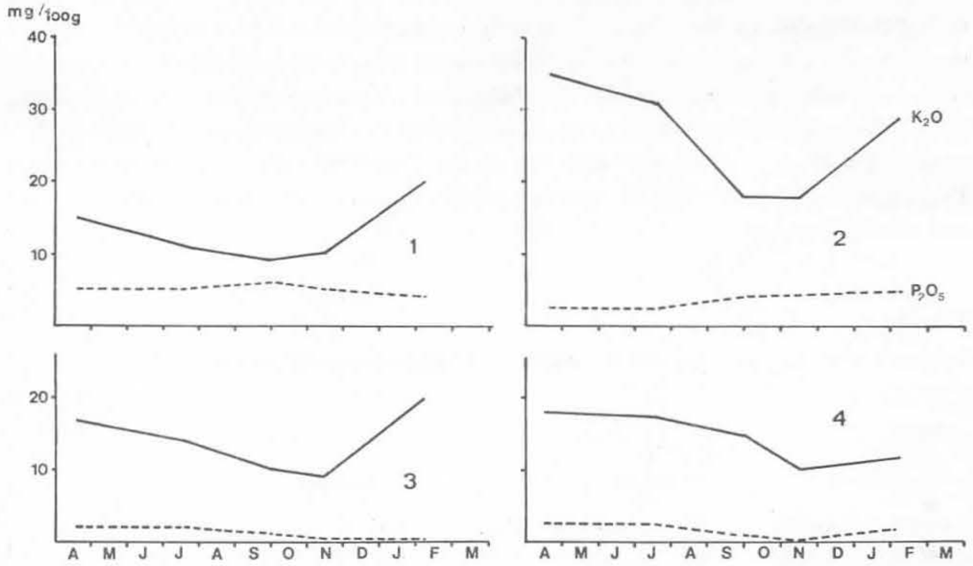

Fig. 7. Dynamics of K_2O content (full line) and P_2O_5 content (dashed line) during the period studied.

Tab. 15.

Values of K_2O (in mg/100 g soil dry matter) estimated on investigated ecotopes

Date		29. 4.	20. 7.	29. 9.	10. 11.	3. 2.	year average
Carici-Festucetum	(E-1)	15.0	11.5	7.5	10.5	20.0	13.3
Lathyro-Quercetum	(E-2)	35.0	31.5	17.5	17.5	34.0	27.1
Seseli-Festucetum	(E-3)	17.0	14.5	10.5	9.5	20.0	14.3
Erysimo-Festucetum	(E-4)	18.0	17.0	14.0	10.5	12.0	14.3

range of 17 to 30 mg/100 g. Similar results are given by SOBOTKA, LANGKRAMER and KHOLOVÁ (1967) for xerothermic communities of Bohemian Karst – about 10 mg/100 g. KOVACS-LÁNG (1966) found in comparable communities in northern Hungary 16 to 30 mg/100 g on limestone, only about 5 mg/100 g on dolomite. The content of K ions in comparable plant communities in South Moravia (limestone), Central Bohemia (Algonkian slates) and České středohoří (basalt) was in the range of 8 to 30 mg/100 g (KUBÍKOVÁ in lit.).

5.1.6. Content of total nitrogen (organic and mineral) in the soil

The estimated results are given in Tab. 16 and Fig. 6.

The estimated content of nitrogen was in the range 0.8 to 1.5 %. The values varied considerably during the year and on different ecotopes and it was not possible to correlate the maximal and minimal values with other estimated factors, edaphic or climatic. Similarly, quite irregular fluctuation of values during two years were found by KUČEROVÁ (1960) on the same locality. BILLÈS, LOSSAINT and CORTEZ (1971) studied the content of mineral nitrogen in the Rendzina soils in the Mediterranean Region, where several years of observations gave curves with quite irregular maximal and minimal values.

Tab. 16.

Values of total nitrogen (in % soil dry matter) estimated on investigated ecotopes

Date		29. 4.	20. 7.	29. 9.	10. 11.	3. 2.	year average
Carici-Festucetum	(E-1)	0.85	0.82	1.41	1.05	1.08	1.04
Lathyro-Quercetum	(E-2)	1.36	0.97	1.45	1.26	1.09	1.22
Seseli-Festucetum	(E-3)	1.49	1.34	0.95	1.20	1.01	1.20
Erysimo-Festucetum	(E-4)	0.83	1.33	1.19	1.29	1.22	1.17

The estimated values may be compared with the results of other authors. Sobotka, Langkramer and Kholová (1967) found a very similar range of N content. In comparable plant communities these values were found: South Moravia (limestone) – 0.5 to 0.7 %, Central Bohemia (Algonkian slates) 0.2 – 1.5 %, České středohoří (basalt) – 0.2 to 0.7 % (Kubíková, in lit.). Kolbek (1973) found in xerothermic communities in České středohoří (basalt and phonolite) 0.07 – 0.15 %. Úlehlová (1964) studied the features of soil under 40 stands of *Stipa* spec. div. The content of nitrogen varied over the broad range of 0.05 to 1.8 %. In the Bohemian Karst she found the values to be about 1 %.

These results show a commonly high content of total nitrogen in soils of xerothermic Rendzina soil subtypes, which is twice as high as the values given for forest soils (about 0.4 %). This is related to the high humus content of these soils and to their characteristic humus forms (see Chapt. 6).

5.1.7. Content of total carbon in the soil

The results are given in Tab. 17.

The content of total carbon is very high in these humus-carbonate soils. The basic share of humus particles in the microstructure of the soil is very clearly seen on soil slides (see Chapt. 6). The greatest particles of humus are macroscopically well differentiated as soil crumbs, which are very stable and do not split.

The values of total carbon range from 12 to 20 %. Sobotka, Langkramer and Kholová (1967) give from comparable communities in Bohemian Karst 3 to 14 %, Kolbek (1973) from xerothermic grasslands in České středohoří 1.8 – 3.5 %, Kubíková (in lit.) from South Moravia (limestone) 15 to 24 %, from České středohoří (basalt) 10 to 18 %, from Central Bohemia (Algonkian slates) 4 to 14 %.

The richest ecotope in carbon on Doutnáč hill is the xerothermic woodland (Ecotope 2) during the whole year; the amount of shed plant material is of course greater in this structurally more complicated community. The rate of cellulose decomposition being decreased on this ecotope (see Chapt. 5.2.5) the amount of deposited plant material in various stages of decomposition becomes accumulated.

Tab. 17.

Values of total carbon (in % soil dry matter) estimated on investigated ecotopes

Date		29. 4.	20. 7.	29. 9.	10. 11.	3. 2.	year average
Carici-Festucetum	(E-1)	16.05	17.55	14.70	16.95	17.1	16.47
Lathyro-Quercetum	(E-2)	19.95	19.95	20.10	19.50	19.65	19.65
Seseli-Festucetum	(E-3)	13.35	14.25	16.05	16.80	14.70	15.03
Erysimo-Festucetum	(E-4)	12.75	16.65	15.30	14.25	13.80	14.55

5.1.8. Content of humus in the soil

The results are given in Tab. 18.

The estimated values of humus content in studied soils reach one quarter to one half of soil dry matter. Úlehlová (1964) found also values reaching up to one half of soil dry matter. Regularly she found the highest values on limestone parent rock, or on basalt. Shales, diabases, sands and loess were found to be much poorer in humus content (2 to 10 %).

Tab. 18.

Dynamics of humus content (in % soil dry matter)

Date	29. 4.	20. 7.	29. 9.	10. 11.	3. 2.	year average
Carici-Festucetum (E-1)	27.60	30.18	25.28	29.15	29.41	28.32
Lathyro-Quercetum (E-2)	34.31	34.31	34.57	33.54	33.79	34.10
Seseli-Festucetum (E-3)	22.96	24.51	27.60	28.89	25.28	25.84
Erysimo-Festucetum (E-4)	21.93	28.63	26.31	24.51	23.73	25.02

The content of stable humus in these Rendzina subtypes is exceeded only by the humus content of subalpine and alpine communities (up to 75 %) and of peats (90 to 100 %) (see Rusek, Úlehlová and Unar, 1975). The reason for humus accumulation on these ecotopes is the same – microclimatically and hydrologically conditioned decrease of further mineralisation.

5.1.9. Ratio of C : N

The results are given in Tab. 19 and Fig. 8.

The C : N ratio is taken for the measure of humus quality; the lowest values characterizing the best developed humus form, the mull. The values found range

Tab. 19.

Dynamics of the C/N ratio

Date	29. 4.	20. 7.	29. 9.	10. 11.	3. 2.	year average
Carici-Festucetum (E-1)	18.88	21.40	10.39	16.20	17.00	16.77
Lathyro-Quercetum (E-2)	14.69	20.65	13.86	15.47	18.26	16.58
Seseli-Festucetum (E-3)	8.91	10.60	16.89	13.95	14.70	13.01
Erysimo-Festucetum (E-4)	15.36	12.51	12.85	11.06	11.00	12.55

from 9 to 21 in the grassland, from 13 to 20 in the woodland. Similar values were found by Sobotka, Langkramer and Kholová (1967) for comparable communities in the Bohemian Karst.

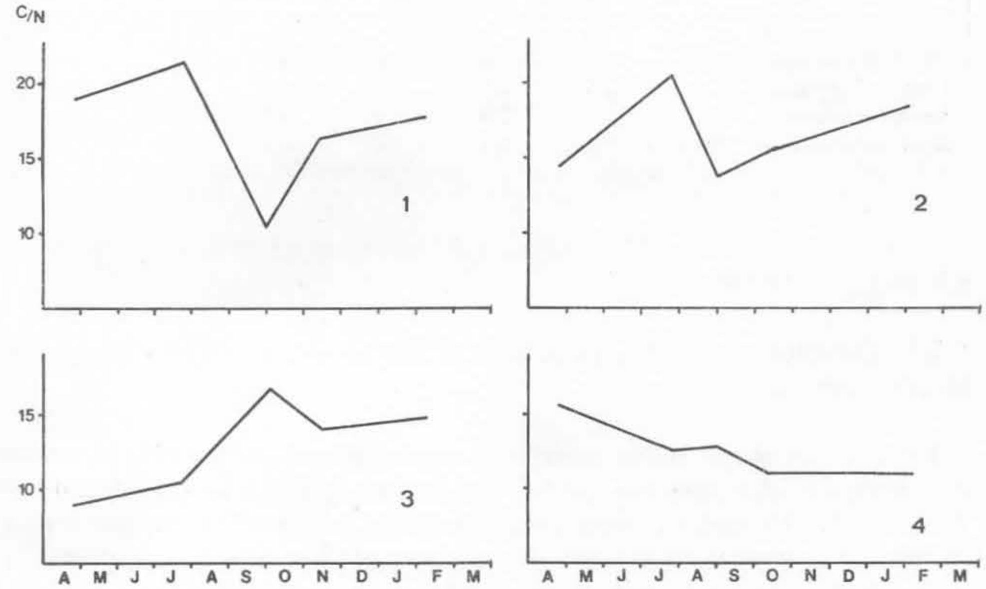

Fig. 8. Dynamics of C/N ratio during the period studied.

Our results mostly coincide well with the humus forms recognized on various ecotopes studied. The soils with the mull-like humus forms of grasslands had lower values of C : N ratio than woodland soils with moder humus form (see Chapter 6).

5.1.10. Content of $P_2 O_5$ in the soil

The results are given in Tab. 20 and Fig. 7.

The soils are very poor in soluble phosphorus when compared with the phosphorus content of agricultural soils. The relatively highest values were found in the grassland *Carici-Festucetum sulcatae*, the rocky grassland *Seseli-Festucetum duriusculae* had only traces of soluble phosphorus.

Sobotka, Langkramer and Kholová (1967) found similar low values in comparable plant communities in the Bohemian Karst (about 5 mg/100 g). Kubíková (in lit.) found for xerothermic grassland communities in Prague suburbs values in ranges of 3 to 16 mg/100 g. All these analysis show that low phosphorus content is characteristic for the first developmental stages of xerothermic Rendzinas.

Tab. 20.

Values of P_2O_5 (in mg/100 g soil dry matter) estimated on investigated ecotopes

Date		29. 4.	20. 7.	29. 9.	10. 11.	3. 2.	year average
Carici-Festucetum	(E-1)	5.0	5.0	6.0	5.0	4.0	5.0
Lathyro-Quercetum	(E-2)	2.5	2.5	4.0	0.0	5.0	2.8
Seseli-Festucetum	(E-3)	2.0	2.0	1.0	0.0	0.0	1.0
Erysimo-Festucetum	(E-4)	2.5	2.5	1.0	0.0	2.0	1.6

5.2. BIOTIC FACTORS

5.2.1. Development of vegetation on the model ecotope during the studied period

The communities on studied model ecotopes are natural, only slightly influenced by human activities. They are relatively stable, their further succession is hindered due to relief and mezo- and microclima. Nevertheless, these xerothermic communities go through frequent cyclic changes. The character of these changes is dependent to some extent on the life form spectrum on different ecotopes studied (see Fig. 9).

The differences in this spectrum with varying share of phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes determine the aspect of the stand and its changes during the year.

The phenology of vegetation during the studied year is given in graphic form in Fig. 10 (simplified). The figure shows that the groups of therophytes, geophytes and phanerophytes have relatively simple life cycles, no repeated or prolonged flowering was observed. On the contrary, some hemicryptophytes and chamaephytes always react with renewed growth of vegetative organs and repeated flowering when the dry season is followed by a humid season under suitable temperature conditions. During the studied period repeated flowering was observed at the end of August and at the beginning of November. Only some smaller or greater part of the populations reacts in this manner. Repeated flowering was observed in species *Stachys recta*, *Helianthemum ovatum*, *Pulsatilla pratensis*, *Bupleurum falcatum*, *Asperula cynanchica* etc.

During the winter, the xerothermic grasslands are characterized by a group of chamaephytes with ever-green leaves forming the winter aspect of these ecotopes. *Carex humilis*, *Potentilla arenaria*, *Sedum boloniense*, *Sedum album*, *Helianthenum ovatum*, *Thymus praecox*, *Alyssum montanum*, *Teucrium chamaedrys*, *Salvia pratensis*, *Verbascum lychnitis*, *Artemisia campestris* and mosses like *Thuidium abietinum*, *Tortella tortuosa* and *Rhytidium rugosum* belong to this group. On the border between chamaephytes and hemicryptophytes are some perennial grasses like *Festuca pallens*, *Festuca valesiaca*, *Festuca sulcata*, *Stipa capillata*, *Stipa joanis*, *Koeleria gracilis*,

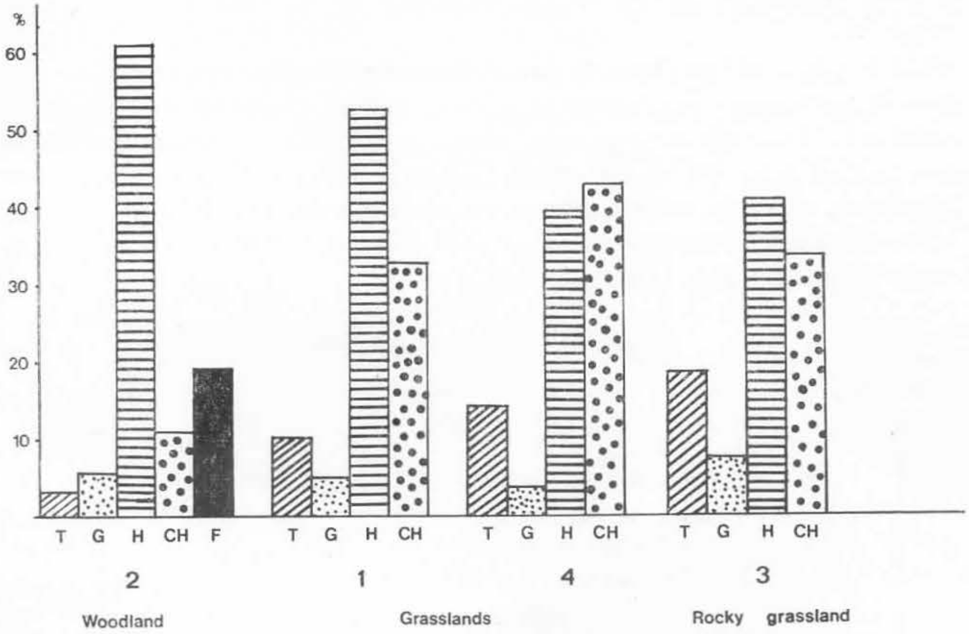

Fig. 9. Relative frequency of different life forms on the ecotopes studied. T - therophytes, G - geophytes, H - hemicryptophytes, CH - chamaephytes, F - fanerophytes.

Melica transsilvanica. At least the inner leaves of the tussocks of these grasses stay ever-green during the winter.

In the thermophilous woodland only population of *Primula veris*, *Hepatica nobilis* and *Teucrium chamaedrys* passed the winter with some small number of green leaves.

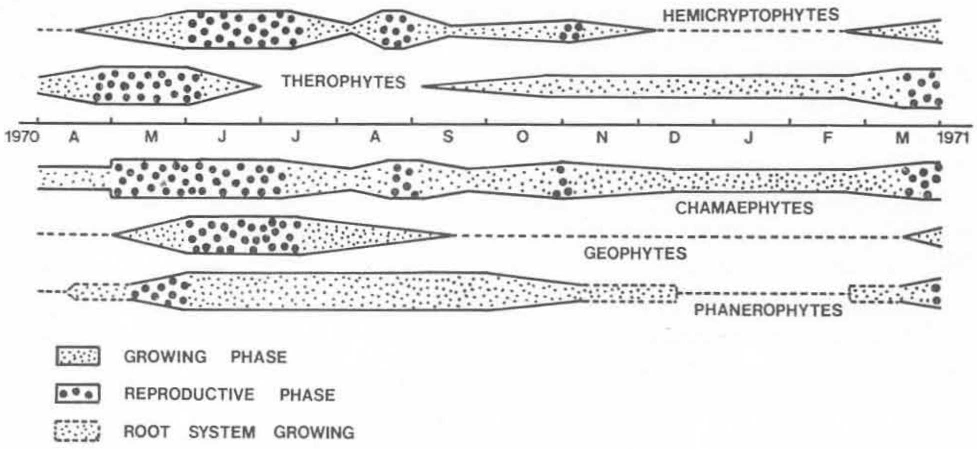

Fig. 10. Phenology of vegetation on Doutnáč hill grouped according to life-forms during the period studied.

5. 2. 2. Dynamics of soil fauna development

The method used (see Chapt. 3) permits the evaluation of the dynamics of development of *Arthropoda* mesoedaphon on ecotopes studied. To get more details of the population dynamics, more samples would be necessary; however, quantitative samples from main seasons, e. g. spring, summer, autumn, and winter give adequate information about the maxima and minima of the populations.

The changes of abundance and biomass of *Oribatei*, "other *Acarina*" and *Apterygota* are given in Figs. 11 and 12.

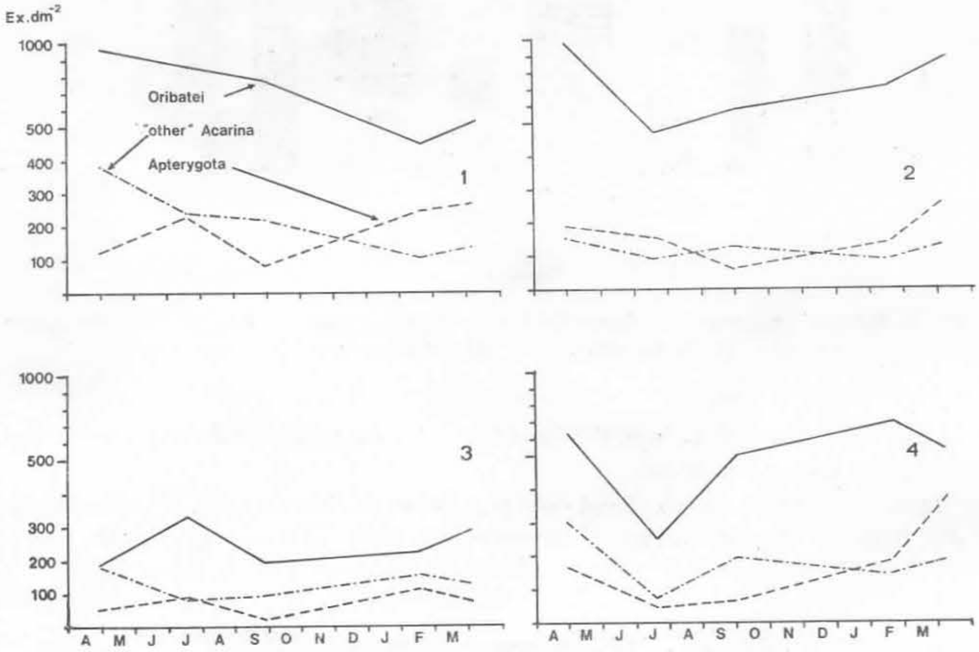

Fig. 11. Dynamics of soil mesofauna abundance during the period studied plotted in the groups *Oribatei*, "other *Acarina*" and *Apterygota*.

Ecotope 1, grassland, *Carici-Festucetum sulcatae*. The abundance of *Oribatei* was not influenced by summer high temperatures and low humidity, their biomass was even higher than in the spring. Their abundance and biomass was gradually lowered during autumn and winter season with rapid increase of abundance in spring 1971, caused by hatching of nymphae. The biomass was not influenced by this process. The curves of abundance and biomass are similar in "other *Acarina*", with absolute values being much lower.

No relation could be found between the abundance and biomass of *Oribatei* and "other *Acarina*" and soil moisture (see Fig. 5 – dynamics of soil moisture in percent of maximal water capacity).

The curve of abundance of *Apterygota* reaches minimum at the end of September, maximum in summer and winter. This course coincides very well with the curve of soil moisture (see Fig. 5) showing the minima of momentary soil moisture at the end of September. The value of the biomass was not influenced being the same as in July. This was caused by the different development of the populations of different species. Populations of some species with high abundance (*Sphaeridia* sp., *Isotomodes productus, Onychiurus armatus, Cryptopygus bipunctatus* etc.) became almost extinct towards the autumn. On the contrary, some other species appeared or grew adult with greater body weight and subsequently with higher biomass, e. g. *Lepidocyrtus lanuginosus, Orchesella multifasciata, Seira* sp. These are species specially adapted to a dry environment. In the winter and spring season 1971 the high biomass is formed by populations of smaller species with high abundance (*Cryptopygus bipunctatus, Onychiurus armatus, Metaphorura bipartita, Isotoma notabilis*).

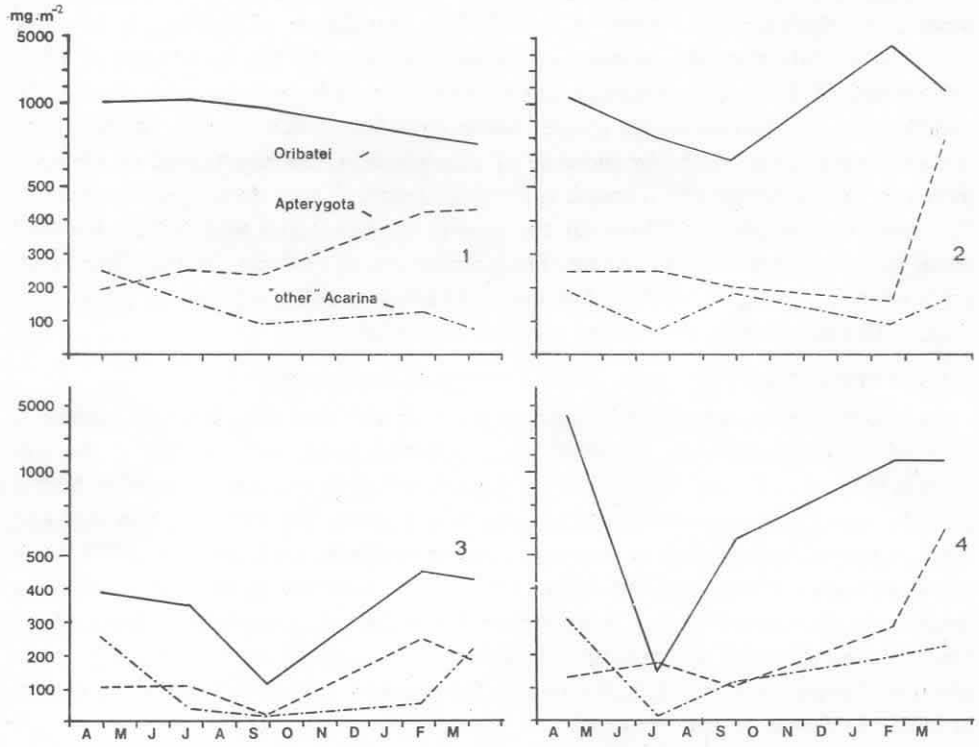

Fig. 12. Dynamics of soil mesofauna biomass during the period studied.

Ecotope 4, grassland, *Erysimo-Festucetum valesiacae.*

The curves of abundance of soil mesofauna are quite different from these found on Ecotope 1. Although the appearance of these two stands is similar and the soils have relatively deep A horizon, the steeper slope inclination determines different ecological conditions of this locality. They are manifested in plant cover, forming a different association (see Chapt. 4.2), as well as in soil mesofauna. This ecotope has very small ability to balance the fluctuations of temperature and precipitation. Thus the minimum of precipitation in July 1970 together with the preceeding dry period and temperature maximum (see Fig. 2) caused deep decrease of abundance and still deeper decrease of biomass in *Oribatei* and "other *Acarina*". The abundance of *Apterygota* is at its minimum in July also; the decrease of biomass is veiled by the occurrence of adult individuals of *Orchesella multifasciata* having very high body weight. *Orchesella multifasciata* is a distinct steppe species, occuring in Pannonicum and in the Southern Russia steppe zone. With the increase of precipitation, the abundance of *Oribatei* increases very quickly; the increase in "other *Acarina*" and *Apterygota* is gradual. The most favourable conditions for the growth of *Apterygota* and "other *Acarina*" occur here during the spring season. The populations of *Oribatei*, on the other hand, are hindered only by the dry and hot summer period, in other seasons the population level of this important soil-forming group is very high.

Ecotope 3, rocky steppe, *Seseli-Festucetum duriusculae*.

The ecological conditions are most extreme on this ecotope. The soil surface is covered only incompletely by plants, thus opening appr. one quarter of the soil surface to direct climatic influence. The shallow soil profile is water-logged in humid periods, desiccated after several clear days (see Fig. 5). The differences in day and night temperatures are high in summer, extreme in winter, oscilating around freezing point. In sunny winter days the melted soil may be warmed up to +15 °C, at night freezing again. These high day temperatures bring the soil mesofauna to full activity. Only limited number of organisms is able to accomodate itself to these extreme ecological conditions, which is the reason for the very low abundance of all groups of soil mesofauna on this ecotope.

The moisture conditions were favourable during the spring and summer season 1970; that caused the maximal abundance of *Oribatei* and *Apterygota*. The dry period at the end of summer caused deep decrease of abundance and biomass in all studied groups of mesofauna. During the autumn and winter gradual increase of abundance and steeper increase of biomass was found in *Oribatei* as well as in *Apterygota*.

Ecotope 2, thermophilous oak-wood, *Lathyro-Quercetum pubescentis*.

The abundance of all studied groups of soil mesofauna, e. g. *Oribatei*, "other *Acarina*", *Apterygota* is highest in the spring. *Oribatei* significantly dominate "other *Acarina*" and *Apterygota*. The abundance of *Oribatei* rapidly decreases in summer and gradual increase occurs during the end of summer, autumn, to winter, when the maximum is achieved. The biomass of *Oribatei* is much higher here than any value found on grassland ecotopes No. 1,3, and 4. It is caused also by the occurence of woodland species, having greater body weight than steppe ones.

The decrease of abundance in *Apterygota* proceeds gradually during summer reaching its minimum in September; this was followed by gradual increase in abundance during winter season, however, with small decrease of biomass. Rapid increase of abundance and biomass occurs in early spring due to the development of the populations of *Folsomia quadrioculata* and *Onychiurus armatus*.

The curve of abundance of "other *Acarina*" has no striking maxima and minima; heir biomass is highest in the spring and late summer season.

On the basis of the samples taken according to above described methods, only very rough conclusions may be made about the dynamics of soil macrofauna (see Tab. 5–8). To get more detailed data it would be necessary to take much greater volumes of soil samples.

Soil mesofauna is characterized by relatively very quick, nonsynchronized alternation of generations during a year. The development of *Collembola*, for instance, may last about one month from the egg to the adult animal. The same is true for mites (*Acarina*).

In soil macrofauna the developmental cycles are mostly much longer, there are only one or two generations in one year, some groups develop even for more years. The course of abundance and biomass of soil macrofauna is therefore different from that of soil mesofauna and also different factors have influence on it. RŮŽIČKA (1968) studied the course of abundance of *Diplopoda* on grassland steppe in Bohemian Karst. He found the lowest abundance of *Leptophyllum nanum* and *Chromatoiulus unilineatus* in dry summer season in July and August (of *Chromatoiulus unilineatus* also in September). This decrease was connected with conspicuous migration from upper A_0 horizon to deeper soil layers.

In the xerothermic area of Austria the soil mesofauna (*Apterygota*, *Acarina*) was studied by Haybach (LOUB and HAYBACH 1967) and by SCHALLER (1949). They found extreme decrease of abundance in summer season in Rendzina soils of this xerothermic area, comparable with Bohemian Karst in its climatic, floristic and faunistic conditions. They explain this decrease by extreme drought and warmth.

Our results show, that also in the same climatic area the effect of macro- and mesoclimate may be profoundly changed by the special habitat conditions of the ecotope studied. The main influence has the microclimate of the certain ecotope, which is strictly connected with the slope inclination and the structure and cover of the vegetation.

5.2.3. Dynamics of the development of the microorganisms

The total numbers of bacteria and fungi were estimated on two nutrient media (see Chapter 3). Therefore, the results contain no detailed information about the presence of specialized fysiological groups of microorganisms. According to the fact, that the method using specific nutrient media for registration of fysiological groups of bacteria has serious hindrance in the ability of one bacterial species to live on various substrates, we decided to limit our observations to two basic nutrient media. The results thus give information about the quantity and behaviour of bacterial and fungus groups able to use these substrata.

5.2.3.1. Dynamics of bacteria in the soil

The results are given in Tab. 21 and Fig. 13.

The total numbers of bacteria correspond well with similar results of other authors. Loub (1960), who studied the microbiological conditions of upper horizons of different soil types, gives for rendzinas values of total numbers of bacteria in the range 3 to 4.10^6 in 1 g soil dry matter; their seasonal fluctuations form a two-peak curve with maximum in spring and autumn and minimum in summer and winter. A similar course of seasonal dynamics was found by Seifert (1960) for humus layers of comparable communities in the Bohemian Karst. He used direct observation of soil extract by fluorescence microscope. The absolute numbers so achieved were 1000 fold higher than numbers registered on nutrient media (3 to 5.10^9 in 1 g soil dry matter).

In our material, the bacterial populations on rocky grassland and neighbouring grassland (Ecotope 3 and 4) clearly show the deep decrease in numbers in the summer, which coincide with the preceeding dry period. In the autumn, numbers of soil bacteria increase regardless of low soil moisture. A quite different course was estimated on Ecotope 1, dense grassland with dominant *Festuca sulcata*. In the summer the peak of the curve was reached, with absolute numbers being 6 times higher than on the rocky grassland. After that, rapid decline occured in the autumn, main-

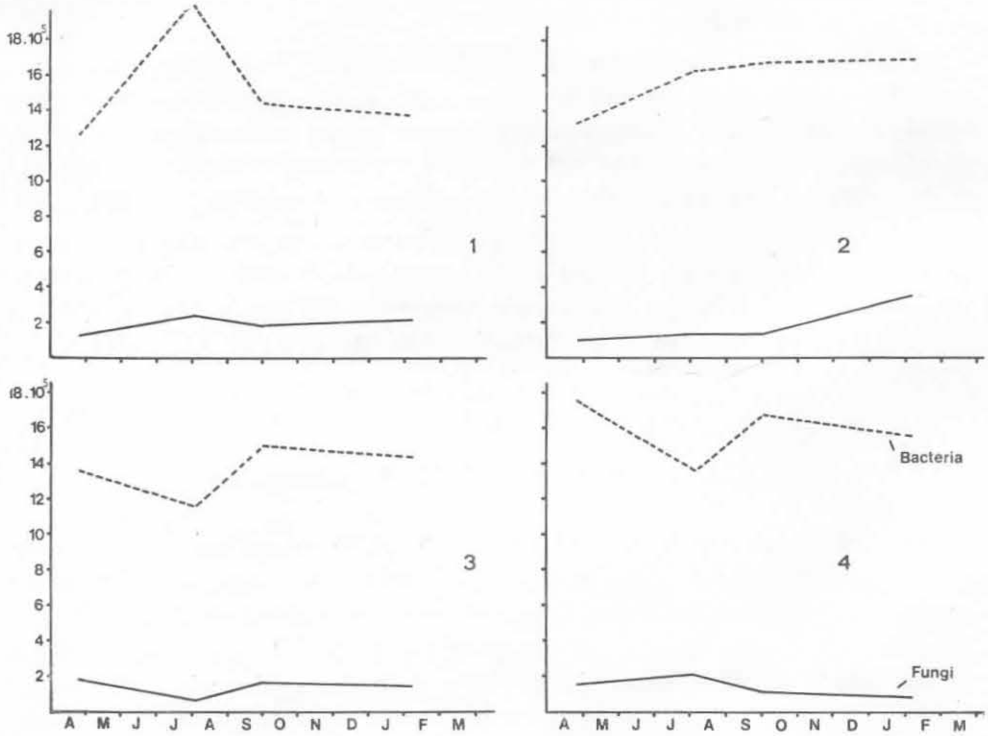

Fig. 13. Dynamics of soil bacteria (dashed line) and fungi (full line) during the period studied.

Tab. 21.

Dynamics of total numbers of bacteria in 1 g dry soil matter ($.10^6$)

Date		29. 4. 1970	3. 8. 1970	29. 9. 1970	3. 2. 1971	year average
Carici-Festucetum	(E-1)	2.64	10.66	4.37	3.8	5.36
Lathyro-Quercetum	(E-2)	3.45	6.24	6.76	6.9	6.09
Seseli-Festucetum	(E-3)	2.77	1.65	4.94	4.34	3.42
Erysimo-Festucetum	(E-4)	6.67	3.74	6.83	5.73	5.74

taining the same population level in the winter. Similarly, high level of the population in the summer season was found in *Oribatei* in this ecotope, thus proving its relative stability of soil conditions. Only prolonged dry period at the end of summer influenced the population numbers of both organism groups. In the woodland (Ecotope 2), the total numbers of bacteria were at their minimum in spring 1970, increased during summer and stayed at the same level during autumn and winter seasons. The absence of summer decrease in bacteria numbers both in Ecotope 1 and 2 points to more mesic conditions common to both of them. SEIFERT (1960) also failed to observe any summer decrease of bacteria numbers in more mesic soil conditions of thermophilous oak wood.

5.2.3.2. Dynamics of fungi in the soil

The results are given in Tab. 22 and Fig. 13.

The fungi, due to the structure of their cell wall, are less sensitive to fluctuations of environmental factors. Therefore, less pronounced decrease in numbers might be observed in their populations during summer, with the exception of the most extreme rocky grassland ecotope. With fungi, an important question arises. With the dilution

Tab. 22.

Dynamics of total numbers of fungi in 1 g dry soil matter ($.10^5$)

Date		29. 4. 1970	3. 8. 1970	29. 9. 1970	3. 2. 1971	year average
Carici-Festucetum	(E-1)	1.11	2.33	1.76	2.09	1.82
Lathyro-Quercetum	(E-2)	1.04	1.41	1.39	3.55	1.85
Seseli-Festucetum	(E-3)	1.83	0.55	1.62	1.37	1.34
Erysimo-Festucetum	(E-4)	1.71	2.15	1.15	0.84	1.46

method, it is impossible to differentiate colonies arising from resting spores or from active mycelia. This can be achieved using specific methods, which was, howewer, outside the scope of this work.

In fungi, profound qualitative changes in the seasonal dynamics of different species populations were found. LOUB (1960) gives for Rendzina soil characteristic summer aspect with dominant species of *Aspergillus* and *Penicillium*. FASSATIOVÁ (1966) confirmed this aspect for grassland ecotope No. 1 on Doutnáč. The species of *Penicillium* and *Aspergillus* are strong decomposers of cellulose. This coincides well with high values of cellulose decomposition found on all three grassland and rocky grassland ecotopes (see Chapt. 6.2.5). In thermophilous woodland the cellulose decomposers appear only during autumn and winter, e. g. species like *Stysanus stemonitis* and *Trichoderma lignorum*. This autumnal and winter aspect in woodland is manifested in the highest numbers of fungi found in our study. Also the cellulose decomposition is highest in the woodland during the winter (see Chapt. 6.2.5) in comparison with other ecotopes.

5.2.4. The activity of soil organisms

The activity of soil organisms was estimated using two criteria: the output of CO_2 from the soil and the cellulose decomposition. For the methods see Chapt. 3.

5.2.4.1. The dynamics of C_2O output from the soil

The results of these measurements are given in Tab. 23 and Fig. 14.

Most authors study this feature on soil samples wetted on 60 % maximal capillar water capacity. In our experiments, we did not change the soil moisture of soil sam-

Tab. 23.

Output of CO_2 (mg CO_2.24 hours^{-1}.100 g dry matter^{-1}) at 22 °C in laboratory conditions and under unchanged momentary soil moisture (see Tab. 10)

Date	10. 5. 1970	9. 6. 1970	20. 7. 1970	29. 9. 1970	10. 11. 1970	3. 2. 1971	5. 4. 1971	year average
Carici-Festucetum (E-1)	33.3	55.5	50.8	33.74	49.14	42.8	43.6	44.12
Lathyro-Quercetum (E-2)	33.9	62.7	44.1	34.6	48.49	58.54	40.86	46.16
Seseli-Festucetum (E-3)	50.0	52.3	52.0	24.3	53.93	64.61	32.10	47.03
Erysimo-Festucetum (E-4)	39.8	61.1	48.1	29.5	45.15	39.17	37.50	42.89

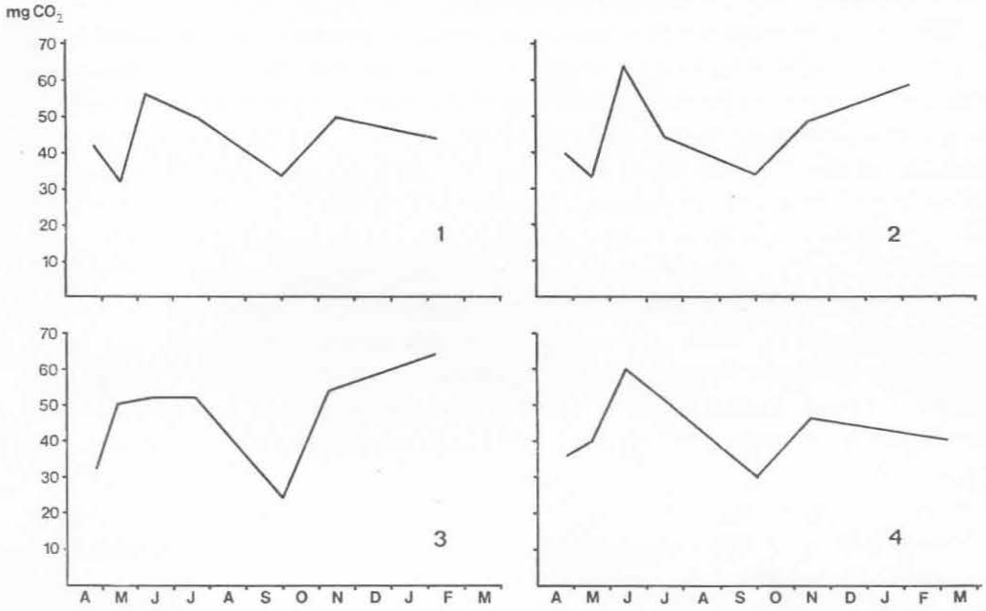

Fig. 14. Dynamics of CO_2 output from the soil during the period studied.

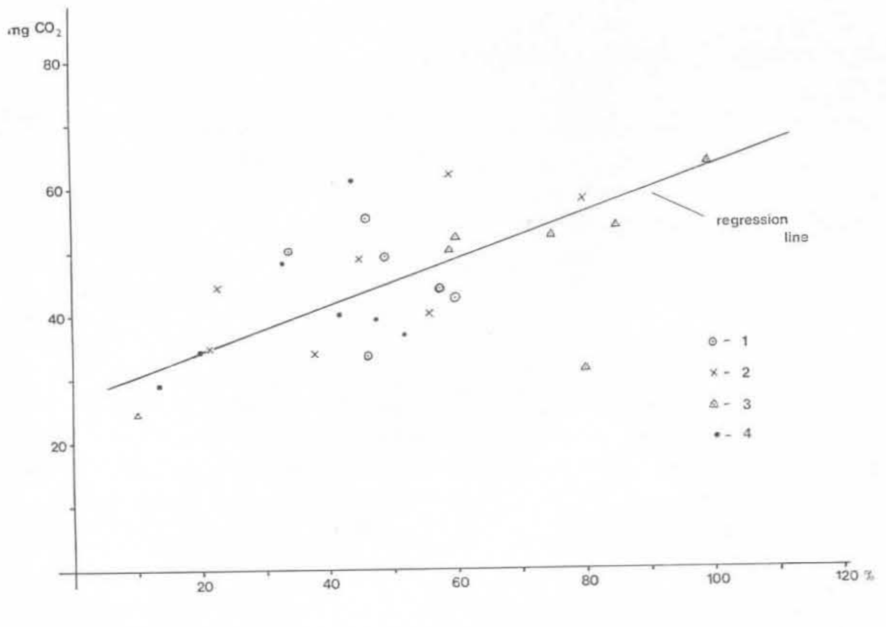

Fig. 15. Regression of CO_2 output on momentary soil moisture (given in % of maximal capillar water capacity) of the ecotopes. The regression coefficient was proved.

ples, we wanted to get information about the actual activity of soil organisms under momentary moisture conditions of the ecotope.

The results have shown that under constant temperature there is direct linear regression of CO_2 output on the soil moisture, see Fig. 15. The significance of the regression coefficient was proved. Out of the regression equation it may be computed that increase in the soil moisture of 10 % maximal capillar capacity causes an increase of the CO_2 output of 4 mg . day^{-1} . 100 g soil dry matter^{-1} irrespective of ecotope. This is true in the range between 20 % to 100 % maximal capillar water capacity. In very wet soil, where also the non-capillar pores are full of water, no further increase in the CO_2 output was found. Also soils very dry enable only retarded activity of soil organisms and the values do not fall in the above pattern. Similar dependence of CO_2 output on soil moisture, not precisely calculated, was found by SEIFERT (1960) for Rendzina soils in the Bohemian Karst. The differences of CO_2 output between studied ecotopes may be therefore explained on the ground of direct dependance of soil organisms on moisture conditions. Regular autumnal decrease of CO_2 output fits well into this pattern.

CALLÉJA (1969) studied the CO_2 output in three mediterranean thermophilous communities – *Brachypodietum ramosi*, *Cocciferetum* and *Quercetum ilicis*. She incubated the samples wetted on optimal soil moisture at constant temperature for 5 days. Her absolute results are different from ours, but the course of the curves shows tendency to some decrease in the dry summer period.

5.2.4.2. The cellulose decomposition

The dynamics of cellulose decomposition on studied ecotopes is given in Fig. 16 and Tab. 24.

Tab. 24.

Cellulose decomposition (in mg.dm^{-2}.day)

Date	29. 4.—9. 6. 1970	20. 7.—8. 9. 1970	29. 9.—3. 12. 1970	3. 2.—5. 4. 1971	year average
Carici-Festucetum (E-1)	5.21	8.97	8.67	0.62	5.86
Lathyro-Quercetum (E-2)	0.19	6.89	4.35	2.45	3.47
Seseli-Festucetum (E-3)	5.80	9.52	9.75	0.08	6.28
Erysimo-Festucetum (E-4)	2.44	7.63	9.47	0.57	5.03
Average day temperature and precipitation on Beroun climatic station during the period of incubation	11.74 °C – 1.6 mm	17.7 °C – 2.88 mm	7.7 °C – 1.45 mm	1.85 °C – 0.73 mm	

There are remarkable differences in cellulose decomposition rates found in grasslands, rocky grassland and thermophilous woodland.

The highest average of the decomposition rates during the studied period was found on the rocky grassland, Ecotope 3. This community is subdued to greatest fluctuations in moisture and temperature in summer as well as in winter. Many authors have shown that mainly the changing water conditions have stimulatory effect on various activities in the soil, e. g. on nitrification. The cellulolytic activity may be further example. This soil feature together with a population of strong cellulose decomposers (fungi of the genera *Penicillium* and *Aspergillus*) causes high cellulose decomposition during summer (9.5 mg . dm^{-2} . day^{-1}). In the winter, on the contrary, the population of cellulose decomposers decline, the shallow soil horizon is deeply frozen and the cellulose decomposition falls to the lowest value found (0.08 mg . dm^{-2} . day^{-1}).

The course of cellulose decomposition is similar on two other grasslands with the peak in summer and autumn and minima in spring and winter. The decrease in winter was not so sharp due to more stabilized soil conditions.

A quite different course of cellulose decomposition was found in the woodland. The minimum occured in the spring 1970 (0.19 mg . dm^{-2} . day^{-1}) followed by rapid increase towards the maximum in summer. During autumn and winter the decomposition was less rapid, but a moderatelly high rate was maintained throughout the whole winter. This is associated with specific populations of cellulose decomposers on this ecotope (see Chapt. 5.2.3.2).

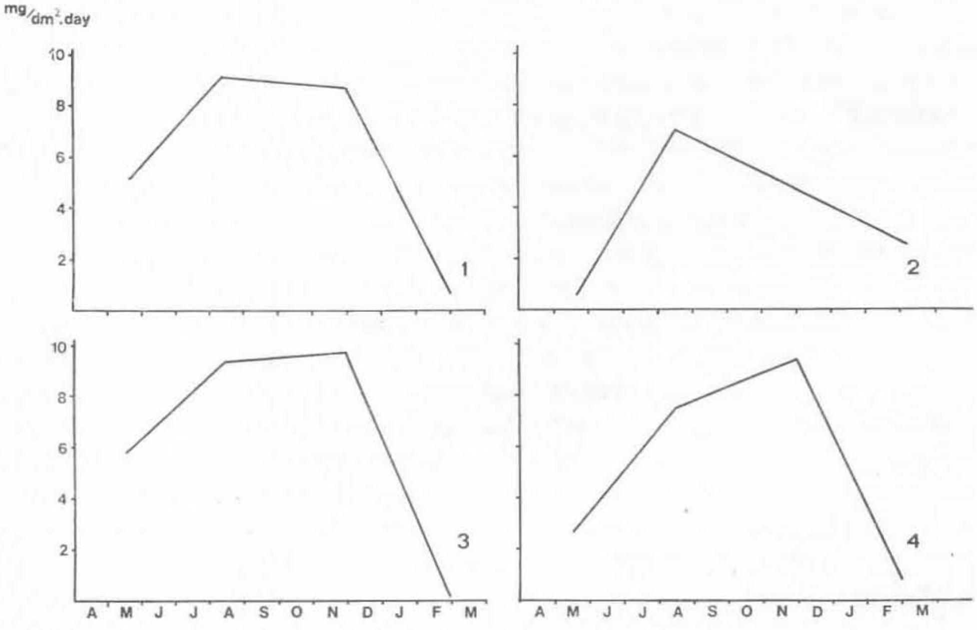

Fig. 16. Dynamics of cellulose decomposition during the period studied.

Similar seasonal dynamics were found by Tesařová and Úlehlová (1968), Tesařová (1970) and Úlehlová (1973) in meadow soils in South Moravia. In their communities they found also the maximal cellulose decomposition during summer months. In communities, whose soil was not frozen during the winter, the cellulose decomposition proceeded also in the winter. The absolute values of cellulose decomposition, however, were much lower than in our tests.

The rate of cellulose decomposition is the result of joint work of cellulolytic bacteria and fungi and of soil micro-, meso- and macrofauna as well. The soil animals, when feeding on cellulose of plant remnants or on filter paper in experimental nylon bags, split the cellulose in small pieces. The intestinal microflora in the body of the soil animal partly decomposes the cellulose, but the greater part of it is excreted from the body as pellets. The pellets contain plant remnants, mineral particles and they are enriched by enzymes and other organic substances, which again form favourable media for soil fungi and bacteria. This process means a substantial increase of cellulose decomposition rate in the soil (see for instance Törne, 1966, Naglitsch and Grabert, 1968).

5.3. THE INTERRELATIONSHIPS BETWEEN THE DYNAMICS OF BIOTIC AND ENVIRONMENTAL FACTORS

The modern concept of ecosystem is derived from mutual balanced interrelationships between biota and environment. These interactions are best seen during the study of successional series. During the succession, gradual change of one or more ecological factors occurs. These changes are immediately followed by the changes of plant and animal components and of the soil features as well. The soil micro- and macrostructure, pH, temperature and moisture, content of mineral and organic substances are being changed. The well differentiated stages indicate the relation between the values characteristic for biotic and environmental components of the ecosystem.

In our study, the rocky grassland, *Seseli-Festucetum*, on one side and the thermophilous oak-wood, *Lathyro-Quercetum*, on the other side represent extreme points of xerothermic successional series in the Bohemian Karst. The thermophilous grassland forms the link between these two extreme points. Some of the factors studied have seasonal dynamics without distinct, well explainable relations; in some others, their interrelationship is very well marked. Such example may be the regression of CO_2 output on momentary soil moisture. The soil moisture, of course, acts here only indirectly effecting the dynamics of soil organisms. Furthermore, under dry soil conditions, the soil organisms are in anabiosis and their respiration is in minimum. Also under humid conditions above 90 % maximal water capacity, the resource of oxygen in soil diminishes together with the living space and the activity of organisms is hindered.

The correlations between the factors studied could be statistically evaluated in a more detailed study. As was already explained in the introduction, we wanted to estimate the conditions of environment and biota in different year seasons. Therefore we compared the results with respect to the trends of seasonal dynamics. To show the conditions of ecological successional series we proceed in the following chapters from the initial stage (Ecotope 3), through the middle stage (Ecotope 4 and 1) to the most advanced stage of the xerothermic series (Ecotope 2). The course of mesoclimate and the course of momentary soil moisture are taken as a basis for comparison.

5.3.1. Relations between different factors on Ecotope 3 (*Seseli-Festucetum duriusculae*)

The course of the annual curve of the following factors agree with that of the momentary soil moisture (also with regard to the course of precipitation and temperature – Fig. 2):

Abundance and biomass of *Apterygota*
Abundance and biomass of *Oribatei*
Biomass of "other *Acarina*"
CO_2 output
Total nitrogen content
K_2O content

The following factors are sensitive to moisture decrease and temperature increase in June and July:

Abundance of "other *Acarina*"
Numbers of bacteria
Numbers of fungi

An inverse curve with regard to that of the momentary soil moisture was observed in following factors:

Cellulose decomposition
C content
Humus content
Ratio C/N

From the survey of these relations it may be derived, that the limiting factor on this ecotope is soil moisture, whose shortness effects marked decrease of numbers, biomass and activity of soil organisms. Soil bacteria and fungi are most sensitive on every longer and shorter fluctuation in soil moisture. Also "other *Acarina*" react in the same manner. Somewhat more resistant are *Oribatei*, being strongly sclerotized and *Apterygota* being composed of many xerothermic forms. Marked decrease of their abundance and biomass occurs only after a long-lasting period of extreme summer drought. The decrease of soil organism abundance is in direct correlation with the decrease of CO_2 output. The decrease of total nitrogen and K_2O content is connected with the total decrease of biological activity of plants and all other soil organisms. In connection with low activity of all edaphobionts the increase of humus content and the deterioration of C/N relation occurs. On the contrary, the cellulose decomposition is highest during the summer season. Regardless of the fact that the population of soil animals is about one third lower than in the spring optimum, the soil animals play very important role in cellulose decomposition (see Chapt. 6).

Specific populations of cellulolytic microflora developing during the summer season (see Chapt. 4.2.3.2) are also important here. What really causes the activation of cellulose decomposers in the summer season, when all other processes are limited, is yet unknown. There is insufficient data about microclimate (the effect of night cooling, of night dew, of short lasting precipitations etc.) and about the bionomy of soil organisms as well.

5.3.2. Relations between different factors on Ecotope 4 (*Erysimo-Festucetum valesiacae*)

The course of the annual curve of the following factors agree with that of the momentary soil moisture (with regard to the course of precipitation and temperature – Fig. 2):

Biomass of *Apterygota*
Abundance of fungi
CO_2 output
CaO content

An inverse curve with regard to that of momentary soil moisture was observed in following factors:

Cellulose decomposition
C content
Humus content

Different curves were observed with following factors:

Abundance of *Apterygota*
Abundance and biomass of *Oribatei*
Abundance and biomass of "other *Acarina*"
K_2O content
Total nitrogen content
Ratio C/N

The temperature and moisture conditions on the grassland Ecotope 4 *Erysimo-Festucetum* are less extreme than on the rocky grassland Ecotope 3, which is manifested by different plant cover and different soil fauna. *Erysimo-Festucetum* is characterized by the decrease of abundance and biomass in the majority of studied groups of soil organisms already in early summer period, on the contrary, an increase of populations occurs to the end of summer. Only the course of biomass of *Apterygota* and of the abundance of soil fungi is different, the population decrease occurs in late summer in connection with the course of momentary soil moisture. CO_2 output agrees basically with the course of soil moisture. Some discrepancy appears in comparison of the courses of CO_2 output and of the abundance and biomass of soil mesofauna in the late summer period. The decrease of CO_2 output may be explained by momentary decrease of the activity of soil organisms in dry environment. The cellulose decomposition and the increase in humus content are effected similarly as on Ecotope 3. The course of the curves of total nitrogen content, of K_2O content and of C/N ratio could not be explained on the ground of present results. Although most care was taken to get well mixed up samples from homogeneous area, the influence of soil heterogeneity cannot be excluded.

5.3.3. Relations between different factors on Ecotope 1 (*Carici-Festucetum sulcatae*)

The course of the annual curve of the following factors agree with that of the momentary soil moisture:

Abundance of *Apterygota*
Biomass of "other *Acarina*"
Abundance of bacteria
Abundance of fungi

CO_2 output (with exception of spring decrease following the long lasting low winter temperatures)

C content
Humus content
K_2O content
Ratio C/N

An inverse curve with regard to that of the momentary soil moisture was observed in following factors:

Total nitrogen content
Cellulose decomposition

A different course was observed with the following factors:

Abundance of *Oribatei*
Abundance of "other *Acarina*"
Biomass of *Apterygota*
CaO content

Ecotope 1 is fysiognomically similar to Ecotope 4, but the lesser slope of this habitat lowers the value of the potential direct solar irradiation (see Chapt. 4.1). This assists the development of dense *Festuca sulcata* tussock-cover and other herbaceous plants which further protect the soil surface from sun radiation and water evaporation. Therefore, many factors studied are not influenced by summer's dry and hot period. The course of abundance of *Oribatei* and "other *Acarina*" shows continual decrease from spring to winter, in the following spring increasing again. *Apterygota* are more sensitive to the course of momentary soil moisture, which may be seen in the course of their abundance and less expressive in the course of their biomass. In the same manner, by decrease of their biomass, "other *Acarina*" react. Bacteria and fungi respond to the permanently favourable soil moisture during the spring and early summer period by the maximal numbers in the July sample. The course of C content, humus content and C/N ratio show distinctly on favourable conditions for uninterrupted continuation of decomposition processes during the whole summer. This feature proves, that the soil moisture is sufficiently high here even during the dry summer period and that it does not act as a limiting factor for decomposition processes and of the development of the majority of soil organism groups.

5.3.4. Relations between different factors on Ecotope 2 [*Lathyro* (*versicoloris*)-*Quercetum pubescentis*]

The course of the annual curve of the following factors agrees with that of the momentary soil moisture:

Abundance of *Apterygota*
Abundance of *Oribatei* (with small fluctuations)
CO_2 output
CaO content
Biomass of *Oribatei*
K_2O content
Ratio C/N

An inverse curve with regard to that of the momentary soil moisture was observed in following factors:

Abundance and biomass of "other *Acarina*"
Total nitrogen content
Cellulose decomposition

A different course was observed with following factors:

Biomass of *Apterygota*
Humus content
C content
Numbers of bacteria
Numbers of fungi

This woodland ecotope has many factors different from preceeding grassland stands. Firstly, a much higher content of C and humus has been estimated here during the whole year. The edaphobionts have here sufficient amount of different forms of substrate during the whole year. This substrate has also great retention ability for greater amounts of precipitation water. The abundance and biomass of soil mesofauna is here highest from all the ecotopes studied. Maximum values appear in winter and spring periods in all groups. The same may be said for the myceliar activity of soil fungi, observed directly on the ecotope. This is connected with intensive cellulose decomposition during winter, which proceeds regardless the low winter temperatures. CO_2 output is again in direct dependance on momentary soil moisture. During the summer intensive transformation of humus from the form less favourable to more favourable – judged according to the decrease of C/N ratio from 20 to 13 – proceeds continuously. This process is possible also due to the high content of total nitrogen in the summer.

5.3.5. Some interesting correlations between factors studied

On the basis of the preceeding analysis of various ecotopes and of the comparison of correlations of environmental and biotic factors, the following interesting relationships appeared.

Very striking is the similar course of abundance of *Apterygota* and soil fungi. This proves similar ecological amplitude of both these groups. Some species of *Apterygota* are furthermore dependent on soil fungi for their nutrition. Both groups need sufficient moisture for their growth and contrary to bacteria need longer time for the development of their populations. Therefore, shortlasting precipitations in the dry period have not such effect on these two groups of soil organisms as they have on bacteria (compare LOUB and HAYBACH, 1967).

Negative correlation was observed in some *Apterygota* and "other *Acarina*". The group "other *Acarina*" is namely mostly formed by predators (*Parasitiformes*, *Trombidiformes*) which are feeding on *Apterygota* and other less mobile soil animals and in this manner they effect the course of their abundance. The development of the populations of these predaceous mites (*Acarina*) is directly connected to the preceeding maxima of the *Apterygota* on which they are feeding. A decline of *Apterygota* population caused by unfavourable ecological conditions (drought etc.) is followed by a decline of predaceous mites.

Oribatei suffer from summer drought only on extreme Ecotopes 3 and 4, where their populations decline substantially during the summer. In the spring, autumn and winter the abundance and biomass of *Oribatei* is very high here reaching values similar to those which persist on the other more mesic ecotopes during nearly the whole year season.

The regimes of nitrogen, carbon and the C/N ratio are also different on Ecotopes 3 and 4 on one side and Ecotopes 1 and 2 on the other side. Substantial improvement of humus quality (decrease of the C/N ratio) occurs on ecotopes 1 and 2 during the summer season. Inverse course is true on extreme Ecotopes 3 and 4, where the C/N ratio increases. This points to the accumulation of undecomposed humus during the summer dry period.

6. MICROSTRUCTURE OF SOILS AND ITS DEVELOPMENT ON ECOTOPES STUDIED

6.1. INTRODUCTION

KUBIËNA (1938) was the first to study the microstructure of soils in situ and on soil slides. Thus he founded a new scientific branch, which was followed by many workers and no scientific study of soil is now possible without a series of soil slides showing the microstructure of the soil profile. Soil slides show not only the microstructure of the soil, but also the biological structural changes of plant remains caused by different components of the edaphon. This feature was used already by KUBIËNA (1948) to differentiate humus forms on the ground of the various stages of "decomposition" by edaphobionts. Kubiëna also was the first to establish the relation of certain groups of edaphobionts to certain types of soil microstructure. *Oribatei* and *Collembola*, for instance, predominate in initial succesional stages, where their pellets form the essential part of a shallow soil profile (Feinmoder). The structure of other humus forms is made by different groups of animals such as *Diplopoda*, *Diptera*, *Enchytraeidae*, *Lumbricidae*.

Some of the numerous followers of Kubiëna's studies worked specially on the role of edaphon in the formation of soil microstructure. ZACHARIAE (1965) studied in detail the influence of soil animals on the decomposition of fallen beech leaves, characterized the types of excrements of single groups of edaphobionts and made conclusions about their significance in soil structure formation. Other workers studied either by field observations or by laboratory experiments, the direct role of different groups and species of edaphobionts in the decomposition of plant remains and the formation of typical excrements (DUNGER, 1968).

A somewhat different method of soil microstructure evaluation using the organic or anorganic origin of soil particles, their morphology and the relative abundance of different categories together with the shape of soil cavities was elaborated by BECKMANN and GEYGER (1967). Also BABEL (1971) and MRÁZ (1970) used in their works mainly the morphological differentiation of soil structural particles. In our work we identify the different structures of organic origin according to the animal groups which are forming them.

The soil fauna plays different role in the formation of soil microstructure. The nutritive specialization of different species of various groups of edaphobionts was studied and three main groups of animals playing a role in the decomposition of plant remains were differentiated:

1. microphytophagous animals, 2. macrophytophagous animals and 3. non-specialized animals.

Microphytophagous animals feed on small algae, remains of mosses and lichens, on bacteria and mainly on fungal hyphae. When feeding on these substrates some species of *Collembola*, for example, also ingest microparticles of minerals. Other species, for instance some *Oribatei*, have mouth-parts adapted only for organic nutrition.

Macrophytophagous animals, for instance *Isopoda*, *Diplopoda*, larvae of *Diptera*, larvae of *Coleoptera*, *Enchytraeidae*, *Lumbricidae*, feed mainly on dead parts of higher plants. Together with particles of plant remains they use bacteria, fungi and microfauna living on these substrates and various amounts of different categories of mineral particles.

Non-specialized animals feed according to the momentary nutritive provisions of the environment. They can scrape fungal and bacterial colonies from the decaying leaf surface together with adhering mineral particles, or they may gnaw the cuticle and parenchymatic tissues of the leaves. This group is formed by some species of *Collembola*, *Acarina*, *Diptera*, etc.

According to ingested material, to the size of the animal and to its systematic position, the excrements which it leaves behind differ. Microphytophagous animals have no substantial effect on the formation of soil microstructure, their excrements have no stability in the soil environment and they are further disintegrated. On the contrary, macrophytophagous animals and non-specialized edaphobionts are basic elements for soil microstructure formation. Their excrements are very stable in the soil environment, especially in soil rich in Ca^{2+} ions. By the activity of soil animals the plant remains are cut into small pieces and mixed up with mineral particles and the excrements are enriched by various enzymes. The presence, abundance and activity of different groups of soil animals depend on ecological conditions of the ecotope; thus different soil microstructure develops on different ecotopes.

6.2. THE MICROSTRUCTURE OF SOIL PROFILE ON THE STUDIED ECOTOPES (PLATES 4—16)

The microstructure was studied on soil slides embedded in artificial resin. The description of microstructure was done according to BECKMANN and GEYGER (1967). The following descriptions of ecotopes are arranged according to soil development from a less advanced stage on the rocky grassland (Ecotope 3), to the xerothermic grassland (Ecotope 1,4), and to the most complex soil of thermophilous oak wood (Ecotope 2).

6.2.1. The rocky grassland (Ecotope 3), *Seseli-Festucetum*

Soil subtype — Protorendzina (KUBIËNA 1953), syn. Syrozem-rendsina (MÜCKENHAUSEN 1962)
Humus form — Arthropoden Moder (Feinmoder).
Soil microstructure (sensu Beckmann and Geyger) — missing.
Minerals — limestone (gravel, coarse and fine sand), quartz (coarse and fine sand, silt).
Organic soil particles — plant remains (on the soil surface)
pellets of edaphobionts without minerals: *Oribatei* ⌀ 50 µm, *Collembola* ⌀ 30 µm;
pellets of edaphobionts with mineral particles (quartz only): *Collembola* ⌀ 30 to 50 µm;
exceptionally pellets of edaphobionts with quartz and limestone mineral particles: *Diplopoda* ⌀ 500 µm.
Microflora - fungal hyphae, which grow through the soil pores and connect the animal pellets; some of them were identified as *Endogone* sp. and *Cenococcum graniforme*.

No vertical zonation of the profile exists. All structural humus particles (pellets) and mineral particles are equally mixed up in the shallow soil profile (maximal depth 5 cm). There are no pellets of *Diplopoda* present on open places covered only by some lichens, mosses and ephemerous spring annuals. Their greater proportion may be observed in the soil formed under the tussocks of perennial grasses (*Festuca pallens, Melica transsilvanica*). This affects the horizontal pattern of soil microstructure and makes a transition to the following type of soil microstructure.

6.2.2. The xerothermic grasslands (Ecotope 1 and 4), *Carici-Festucetum, Erysimo-Festucetum*

Ecotopes 1 and 4 are evaluated together, because they have the same microstructure and the same proportion of organic and mineral particles in the soil microstructure.
Soil type — Mullartige rendzina (KUBIËNA 1953).
Humus form — Mullartiger Moder and Mull.
Soil microstructure — Krümmelstruktur (BECKMANN and GEYGER 1967).
Minerals — limestone forming coarse particles, smallest about ⌀ 25 µm, quartz in the category of silt and clay.
Organic soil particles — plant remains and plant roots (very often);
pellets of edaphobionts without minerals: *Oribatei* ⌀ 50 µm, *Collembola* ⌀ 50 µm;
pellets of edaphobionts with minerals (quartz and limestone): *Collembola* ⌀ 100 µm, *Diplopoda* ⌀ 500 µm, *Enchytraeidae* ⌀ 200 µm, *Lumbricidae* ⌀ 1000 to 2000 µm.
Microflora — the soil pores are inhabited by hyphae of soil fungi, out of which *Endogone* sp. and *Cenococcum graniforme* could be identified on soil slides.

Vertical zonation on the slides:

0—2 cm: Arthropoden Moder — pellets of *Oribatei*, *Collembola* and *Diplopoda*;
2—5 cm: Mullartiger Moder — pellets of *Enchytraeidae*, *Diplopoda*, disintegrated pellets of *Oribatei* and *Collembola*, mainly excrements of *Lumbricidae*;
5—20 cm: Mull — excrements of *Lumbricidae*,

The soil microstructure is characterized here by the pellets of *Diplopoda* in the upper part of the soil profile, with relatively lower proportion of pellets of *Oribatei* and *Collembola*. The lower part of the profile is formed by excrements of *Lumbricidae* and *Enchytraeidae*. No marked horizontal pattern was observed.

6.2.3. The thermophilous oak wood (Ecotope 2), *Lathyro-Quercetum*

Soil type — Moderrendzina (MÜCKENHAUSEN 1962).
Humus form — Arthropoden Moder (Grobmoder) and Mull.
Soil microstructure — A_{01} horizon without structure, lower horizons Krümmelstruktur (BECKMANN and GEYGER 1967).
Minerals — the same as described above.
Organic soil particles — plant remains and plant roots — pellets of edaphobionts without minerals: *Oribatei* ∅ 35 µm;
pellets of edaphobionts with minerals: *Collembola* ∅ 75—90 µm, *Enchytraeidae* 120 µm, *Isopoda* 340 × 160 µm, *Diplopoda* 500 µm, *Diptera* 1450 µm, *Lumbricidae* up to 5 mm.
Microflora — conspicuous hyphae of mycorrhizal fungi, some spores of *Endogone* sp.

Vertical zonation on the slides:

0—5 cm: Arthropoden Moder — a layer of free laying pellets of *Diplopoda*, *Isopoda*, *Collembola* (the width of this layer is subject to seasonal fluctuations);
5—15 cm: Mullartiger Moder to Mull — excrements of *Lumbricidae*, *Diptera*, plant mycorrhizal roots, disintegrated pellets of *Collembolc*, limestone skeleton.

The characteristic feature of the soil microstructure in the thermophilous woodland is the great heterogeneity of different types of excrements. The upper part of the profile is formed by coarse Arthropoden Moder which intergrades irregularly at different depths to Mullartiger Moder and to Mull. *Oribatei* (*Phtiracarids*) play a conspicuous part in the disintegration of lignified plant tissues and leaves. Similarly, *Collembola* play an important role in plant leaf decomposition. Larvae of *Diptera* may consume either directly the plant remains, or the pellets of smaller animals. *Isopoda* occur only on ecologically favourable microhabitats and their excrements are therefore less frequently seen on soil slides. They are skeletonizing older dead leaves.

6.3. THE DEVELOPMENT OF SOIL MICROSTRUCTURE ON STUDIED XEROTHERMIC RENDZINAS

The soil microstructure was studied on three different types of rendzina: protorendzina — mullartige rendzina — moderrendzina.

Protorendzina is the initial developmental type of rendzina, which coincides with the simplest composition of soil microstructure formed predominately by the pellets of *Oribatei* and *Collembola*. These are also the soil mesofauna groups having much higher dominancy and biomass than other groups of soil Arthropoda fauna. Also the structure of the plant community is most primitive here.

The xerothermic grassland forming a more advanced ecosystem is characterized by the more complex structure of plant community, by the higher diversity of the soil animal community and by the much more complicated soil microstructure. Higher diversity of soil animal groups is manifested in higher numbers of morphologically different shapes of pellets. Different groups of soil animals inhabit different horizons of soil profile depending on their ecological demands. The more xerothermic species live in upper layers, species sensitive to desiccation inhabit the lower layers of the profile. Different soil layers have therefore specific animal synusia, which leave the remains of their activity in the form of accumulated pellets, excrements and cavities. Thus the vertical differentiation of the profile develops.

The most advanced ecosystem of the studied xerothermic succession series is the thermophilous oak-wood. The structure of plant community is developed in several above ground and subterranean layers, the composition of the soil animal community is most diversified here. This coincides with the development of the soil type microstructure. In comparison with preceeding ecosystems, a further two large groups of soil animals play an important role in the formation of rendzina type: *Isopoda* and especially larvae of *Diptera*. The soil profile has similar horizons as on xerothermic grassland, but the pellets are here of another shape and diameter. Inside the pellets larger fragments of plant remains may be observed. The soil microstructure is influenced also by the different character of plant remains, such as the leaves and branchlets of woody plants. The horizontal mosaic of the vegetation conditions different microhabitats which influence the horizontal changes in the soil microstructure. The soil of this ecosystem is, compared with preceeding types of microstructure, the most complicated.

In the preceeding chapters we have described the successive changes of the plant cover and of the soil animal community. With advancing succession the simple open community of rocky grassland changes into the closed community of grassland and finally into the wood. Similarly, the succession of soil animal communities occurs. The more complicated structure of the ecosystem is followed by soil development manifested in the greater depth of soil profile, in its differentiation into macroscopical horizons and in greater morphological heterogeneity of soil microstructure.

Our results thus agree with generally formulated opinions of KUBIËNA (1948), who says about the soil development: "Entwicklung ist ein Prozess, der von Homogenem zu Heterogenem führt (H. Spencer) oder im Hinblick auf bodenkundliche Verhältnisse formuliert, der von einem wenig Heterogenen zu einem stärker Heterogenen überleitet . . .. Die Art und Weise der Zunahme der Heterogenität zu verfolgen ist die Hauptaufgabe der Entwicklungsforschung."

The mechanical stability of animal pellets on all ecotopes is very high. It is caused very probably by the high amount of Ca^{2+} ions in the soil environment. No structural changes of pellet shape were observed during the year season. The changes in the proportion of pellet types occur in the case, when the pellets of small animals are eaten by larger animals. For instance *Diplopoda*, larvae of *Diptera*, *Enchytraeidae* and *Lumbricidae* feed on pellets of *Collembola* and *Oribatei*; these smaller pellets may often be recognized inside the larger pellets of these bigger animals – see Plate 6 A, 16(2) pellets of *Diplopoda*. Only in some cases, the disintegration of *Diplopoda* excrements into original smaller pellets of *Oribatei* and *Collembola* was observed on soil slides.

On the basis of the study of our slides and on the basis of laboratory experiments with *Collembola*, we cannot agree with the conclusions of ZACHARIAE (1963), who considers *Collembola* without any influence on soil formation. *Collembola* play important role in the formation of primary successive stages of the soil, as we have found in the case of xerothermic protorendzina, where their pellets are highly stable. Similar results were published by KUBIËNA (1948, 1956). Also DUNGER (1968) found in the laboratory the important role of *Collembola* in the decomposition of plant remains. The soil formation activity of *Collembola* is in the higher developmental stages of soil types covered by soil macrofauna, who feeds on them. In these soil types *Collembola* pellets accumulate more expressively only in horizon $A_{0\,r}$, where the ecological conditions are extreme and do not enable the penetration of ecologically more sensitive species of macrofauna during the greater part of the year.

7. CONCLUSIONS

1. The work deals with the developmental series of xerothermic rendzina soil type in the Bohemian Karst, on the model site Doutnáč, and with its interrelationships to other chosen components of the ecosystem. The study dealt with plant communities, soil animal communities, mainly soil Arthropoda communities, total numbers of soil fungi and bacteria, activity of soil organisms (output of CO_2 and cellulose decomposition), soil moisture, pH, content of K_2O, CaO, N, C, P_2O_5. All these biotic and abiotic factors were studied during a one year season from 1970 to 1971 at several intervals. Together with these factors the soil microstructure was studied on soil slides.

2. The study revealed three basic stages of ecosystem development on the southern slope of the studied model site. These three successive stages may be characterized by their physiognomy as the rocky grassland, xerothermic grassland and woodland. Detailed description of the locality is given in Chapter 4. Characteristic species of studied communities and minimal and maximal values of biotic and abiotic factors are summarized in Tab. 25.

3. The annual dynamics of biotic and abiotic factors has pointed to following conclusions: the plant cover distinctly responds to the mesoclima of southern slope of Doutnáč hill and influences quite specific course of microclima on different ecotopes studied. The course of microclima, mainly the course of soil moisture and day and night fluctuations of soil temperature, directly influences the activity of soil organisms, as may be seen on the growth of the population, on the biomass, on the respiration (output of CO_2) and on consumation of nutrition (cellulose decomposition). The fluctuations of mesoclima are only insignificantly corrected by the opened cover of initial plant community and the activity of soil edaphon is thus influenced directly by momentary changes of mesoclima (air temperatures, precipitation). The limiting factor here is the soil moisture, which is subject to greatest fluctuations in this ecotope. These extreme fluctuations cause the poorness and specific species composition of soil organisms and influence also the absolute number of different populations. Significant decrease of population numbers occurs in most organisms during the summer season. On the contrary, specific cellulolytic bacteria and fungi are activated even by short-lasting summer precipitations, what may be seen on the increase of cellulose decomposition rate during the summer season.

The closed plant cover of the xerothermic grassland influences a more balanced soil moisture, so that the soil moisture is sufficiently high here even during the dry summer period and it does not act as a limiting factor for decomposition processes and of the development of the majority of soil organism groups.

The woodland ecotope has many features different from grassland ecotopes. The differences are in the microclima and in the primary production, which influences the quality and quantity of plant remains. From the floristic and faunistic point of view, the woodland ecotope has the highest diversity and the species composition is markedly different from that of the rocky grassland and xerothermic grassland. The abundance, biomass and activity of soil organisms are at their peak in the winter and spring seasons; the values estimated in soil *Arthropoda* are much higher than anything found on grassland ecotopes. The populations of cellulolytic microorganisms are different from cellulose decomposers on grassland ecotopes and they are active also during the winter season. The woodland ecotope is characterized further by intensive transformation of humus forms during the summer season, when a more favourable type of humus is formed (see C/N).

4. Both grassland ecotopes studied, classified as two different phytocoenoses and zoocoenoses, have many common features. Some other features, however, indicate close ecological relations of grassland ecotope 4 (*Erysimo-Festucetum*) to rocky grassland ecotope 3 (*Seseli-Festucetum*) and, on the contrary, relations of grassland ecotope 1 (*Carici-Festucetum*) to the woodland ecotope 2 (*Lathyro-Quercetum*). Similar ecological conditions on ecotopes 3 and 4 cause the summer decrease of *Oribatei* populations. The regimes of nitrogen and carbon are also similar on these ecotopes, and the humus quality deteriorates during the summer season due to the accumulation of undecomposed plant remains. The abundance of soil organisms on ecotope 1 and 2 differs by moderate fluctuations from the preceeding two ecotopes. Also the dynamics of C/N ratio is similar on both these ecotopes and opposite to those of ecotope 3 and 4. These results show the more mesic character of the grassland *Carici-Festucetum sulcatae* which contrasts with the more xerothermic character of the *Erysimo-Festucetum valesiacae*.

5. The developmental series of xerothermic rendzinas on the studied site is composed of three basic subtypes of rendzina: protorendzina (Ecotope 3), mullartige rendzina (Ecotope 1, 4), moderrendzina (Ecotope 2). All these subtypes are characterized by specific microstructure. The microstructure is formed by the excrements and burrowing activity of some groups of soil animals. During the succession, a structurally more complex ecosystem is formed, which supports the existence of higher numbers of ecologically different groups of soil animals. These animals leave therefore long-lasting traces of their activity in the soil. The microstructure of protorendzina is formed mainly by excrements of *Oribatei* and *Collembola*. Mullartige rendzina is composed in upper layers by pellets of *Diplopoda* and *Enchytraeidae*, less by pellets of *Collembola* and *Oribatei*. The lower layers are formed by excrements of *Lumbricidae*. The microstructure of moderrendzina is formed by the excrements of many groups of soil animals including *Collembola*, *Oribatei*, *Diplopoda*, *Isopoda*, larvae of

Tab. 25.

Characteristics of studied ecotopes

Ecotope and No. of locality	Rocky grassland, No. 3	Xerothermic grassland, No. 1, No. 4	Thermophilous oak wood, No. 2
Plant community	*Seseli-Festucetum duriusculae* Klika 1933	*Carici-Festucetum sulcatae* Klika 1951 (E 1) *Erysimo-Festucetum valesiacae* Klika 1933 (E 4)	*Lathyro(versicoloris)-Quercetum pubescentis* (Klika) Jakucs 1960
Characteristic and dominant plant species	*Festuca pallens, Seseli devenyense, Potentilla arenaria, Thuidium abietinum*	*Festuca sulcata, Carex humilis, Thalictrum minus* (E 1) *Festuca valesiaca, Filipendula vulgaris* (E 4)	*Quercus pubescens, Cornus mas, Lathyrus versicolor, Dictamnus albus, Primula veris*
Characteristic and dominant species of soil *Arthropoda*	*Xenylla boerneri, Entomobrya* cf. *handschini*	*Cryptopygus bipunctatus, Sminthurinus aureus, Eosentomon transitorium* (E 1) *Isotomodes sexsetosus, I. armatus, Mesaphorura tenuisensillata, Xenylla boerneri* (E 4) *Onychiurus armatus, Doutnacia xerophila, Isotoma notabilis, Isotomodes productus, Sphaeridia* sp., *Leptophyllum nanum* (E 1 and 4)	*Folsomia quadrioculata, Cryptopygus bipunctatus, Isotomiella minor, Metaphorura affinis, Isotoma notabilis, Lepidocyrtus lignorum, Eosentomon bohemicum*
Characteristic species of soil fungi (according to Fassatiová 1966)		*Aspergillus ochraceus, A. ustus, Penicillium casei, P. frequentans, Fusarium oxysporum, Myrothecium verrucaria* (E 1)	*Absidia heterospora, Penicillium brevicompactum, P. diversum, Fusarium javanicum*
Soil subtype	Protorendzina	Mullartige rendzina	Moderrendzina
Microstructure	Missing, free laying *Arthropoda* pellets	Krümmelstruktur	upper horizon without structure, lower hor. Krümmelstruktur

Minerals	limestone > 0.025 mm quartz 0.2–0.002 mm	limestone > 0.025 mm quartz 0.2–0.002 mm	limestone > 0.025 mm quartz 0.2–0.002 mm
Pellets	*Oribatei, Collembola* 30–50 µm	*Diplopoda* 500 µm *Oribatei* 30–50 µm *Collembola* 30–50 µm *Enchytraeidae* 120–200 µm *Lumbricidae* ⌀ 5 mm	*Diplopoda* 500 µm *Isopoda* 350 µm *Diptera* larv. 1400 µm *Oribatei* 35 µm *Collembola* 30–75 µm *Enchytraeidae* 120 µm *Lumbricidae* ⌀ 5 mm
Maximal capillar water capacity (g/100 g soil dry matter)	80.2	149.5 (E 1) 143.1 (E 4)	115.1
Fluctuations of soil moisture during the studied period (in % of max. cap. water capacity)	9.9 –139.3	17.5 –59.8 (E 1) 24.1 –59.7 (E 4)	22.9 –81.4
Value of pH	7.29–7.8	7.09– 7.6	7.12– 7.7
CaO (% of dry matter)	0.35– 1.08	0.24– 0.81 (E 1) 0.29– 0.78 (E 4)	0.26– 0.93
K_2O (mg/100 g dry matter)	9.5 –20.0	9.5 –20.0 (E 1) 10.0 –18.0 (E 4)	17.5 –35.0
Humus content (%)	22.9 –28.9	25.3 –30.2 (E 1) 21.9 –28.6 (E 4)	33.5 –34.5

Tab. 25 (continued)

N (%)	0.95— 1.49	0.82— 1.41 (E 1) 0.83— 1.33 (E 4)	0.97— 1.45
C/N	8.9 —16.8	10.4 —21.4 (E 1) 11.0 —15.4 (E 4)	13.8 —20.6
Total numbers of soil bacteria (in 1 g soil dry matter)	1.65— 4.94.10^6	2.64—10.66.10^6(E 1) 3.74— 6.83.10^5(E 4)	3.45— 6.90.10^6
Total numbers of soil fungi (in 1 g soil dry matter)	0.55— 1.83.10^5	1.11— 2.33.10^6(E 1) 0.84— 2.15.10^5(E 4)	1.04— 3.55.10^5
Total numbers of soil *Arthropoda* (on 100 cm^2)	*Acarina* 280—420 *Collembola* 20—110	320—1340 40—360	470—1130 60—260
Biomass of soil *Arthropoda* (mg/m^2)	*Acarina* 120—510 *Collembola* 20—250	160—1620 100—440	840—1540 160—780
Desintegration of cellulose (mg/dm^2. day)	0.08— 9.75	0.61— 8.97 (E 1) 0.57— 9.47 (E 4)	0.19— 6.89
CO_2 output (mg CO_2/day. 100 g soil dry matter)	24.29—64.61	33.3 —55.5 (E 1) 29.5 —61.1 (E 4)	33.9 —62.7

Diptera, *Enchytraeidae* and *Lumbricidae*, whose existence is due to the structure of woodland ecosystem.

6. Interrelationships of plant communities, soil organism communities, soil subtypes and various environmental factors were estimated and quantitatively expressed. During the developmental process all components are linked together and changes in one component cause the changes of other components. The first initial stage is characterized by opened mosaic-like plant community with undeveloped vertical structure, low species diversity of soil animal community, and by shallow protorendzina subtype with monotonous microstructure without soil aggregation. When higher layer of protorendzina is accumulated suitable conditions are formed for succession supporting the tussocks of perennial grasses, which in turn form more favourable conditions and microclimate for more sensitive groups of soil organisms. The differentiation of the soil animal community is linked with structurally more complicated soil aggregates. Under this more advanced successional stage – xerothermic grassland – the structurally more complicated soil subtype is formed, the mullartige rendzina. The penetration of woody plants is connected with profound change in light, temperature and moisture regime of the ecotope which is expressed in the change of the herbaceous layer, in the change of quality and quantity of plant remains and in the changing soil animal community. The great diversity in the soil animal community is linked with great heterogeneity of microstructure of rendzina subtype – moderrendzina. Natural elimination of the woody plants or cutting of the wood would cause on these southern slopes a backward degradation of the soil organism community and also of rendzina subtype from moderrendzina to mullartige rendsina and possibly to protorendzina.

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EXPLANATION OF PLATES

Plate 1. A) General view on Doutnáč hill; the irregular open area is the studied rocky steppe and grassland enclosed in the thermophilous oak-wood. B) General view on the rocky steppe, *Seseli-Festucetum duriusculae* (Ecotope 3) in early spring aspect.

Plate 2. A) Detail of vegetation cover on rocky steppe (Ecotope 3); the tussocks of *Festuca pallens, Potentilla arenaria, Cyanus rhenanus* and *Sedum boloniense* may be recognised. B) Detail of vegetation cover of the grassland, *Carici-Festucetum sulcatae* (Ecotope 1). Dominant tussocks of *Festuca sulcata* densely cover and protect the soil surface.

Plate 3. A) Early spring aspect of the thermophilous oak-wood *Lathyro(versicoloris)-Quercetum pubescentis* (Ecotope 2). B) Detail of soil surface of Ecotope 2 in early spring. The soil is covered by fallen oak leaves and pieces of branchlets.

Plate 4. Details of digestive tract of some soil-forming animals. A) A species from the family *Enchytraeidae* — general view with formed-up pellets in the lower part of the intestine. B) Detail of the same specimen; plant tissues and mineral particles may be seen inside the pellets. C) *Passalozetes africanus* (*Oribatei*) with two pellets without mineral particles in the intestine. D) Detail of the central part of the intestine of *Onychiurus armatus* (*Collembola*) with small mineral particles, fungal hyphae, plant tissues and amorphous substance.

Plate 5. A) Microstructure of Protorendzina from rocky grassland (Ecotope 3), characterized by free-laying small pellets of *Collembola* and *Oribatei* (a), particles of limestone parent rock (c), exceptionally by large pellets of *Diplopoda* (d) and cutted plant roots (b). B—C) Pattern of microstructures on the rocky grassland, B) Thin section from the place covered only by therophytes and mosses, C) Thin section below tussocks of perennial grasses. Enlarged: A — 40×, B, C — 10×.

Plate 6. Microstructure of Mullartige rendzina, horizon A_{01} (Ecotope 1); A) normal light, B) polarized light. Circular and elliptic cuts of *Diplopoda* pellets (a), irregular smaller pellets of *Enchytraeidae* (b), small particles of limestone (c) and cutted plant roots (d) may be seen. The large grains of minerals inside the *Diplopoda* and *Enchytraeidae* pellets are seen in the polarized light as glistening spots. Enlarged: 40×.

Plate 7. Microstructure of Mullartige rendzina, horizon A_1 (Ecotope 1); A) normal light, B) polarized light. Characteristic structure of *Lumbricidae* excrements. Organic substance is regulary mixed up with larger and smaller mineral grains (a). Enlarged: 40×.

Plate 8. Microstructure of Moderrendzina, horizon A_{01} (Ecotope 2); A) normal light, B) polarized light. The layers of leaves (a) are mixed up with *Collembola* pellets with mineral particles inside (b), *Oribatei* pellets without mineral particles (c), some *Diplopoda* pellets (d) and irregular excrements of some smaller *Lumbricidae* (e). Enlarged: 20×.

Plate 9. Microstructure of Moderrendzina, horizon A_1 (Ecotope 2); A) normal light, B) polarized light. Local greater accumulation of *Diplopoda* and *Isopoda* pellets with large mineral grains (a). Enlarged: 40×.

Plate 10. Microstructure of different rendzina subtypes: 1. Protorendzina in normal light. 2. Protorendzina in polarized light (pieces of limestone yellow). 3. Moderrendzina — A_{01} horizon. 4. Moderrendzina — a detail of A_{01} horizon. Enlarged: 1. — 30×, 2. — 40×, 3. — 3×, 4. — 8×.

Plate 11. Microstructure of different rendzina subtypes: 1. Moderrendzina — upper part of A_1 horizon with *Lumbricidae* excrements. 2. Mullartige rendzina — upper part of A_1 horizon formed mostly by *Diplopoda* pellets. 3. Mullartige rendzina, lower part of A_1 horizon formed mostly by *Lumbricidae* excrements. Enlarged: 1—3: 10×.

Plate 12. Microstructure of Moderrendzina under thermophilous oak wood. 1. A_{00} horizon, oak leaves decomposed by *Collembola* and *Oribatei*; layers of leaf remains alternating with pellets. 2. Detail showing leaves eaten by *Collembola* (rough pellets) and *Oribatei* (rounded pellets); a part of *Lumbricidae* excrement below. 3. Detail showing *Collembola* pellets between two oak leaves. Enlarged: 1 — 30×, 2 — 70×, 3 — 75×.

Plate 13. Microstructure of Moderrendzina under thermophilous oak wood. 1. A_{01} horizon, a piece of wood eaten by *Oribatei*, larger pellets of *Diplopoda* are seen around; normal light. 2. The same slide in polarized light showing the presence of minerals in larger pellets. 3. A detail showing the preferrence of *Oribatei* to certain plant tissues; normal light. 4. The same detail in polarised light showing the absence of minerals in *Oribatei* pellets. Enlarged: 1—2: 15×, 3—4: 45×.

Plate 14. Types of soil animal pellets. 1. Rounded *Diplopoda* pellets with large mineral particles inside, *Carici-Festucetum sulcatae*; normal light. 2. The same slide in polarized light showing the inner structure of pellets. 3. A part of *Lumbricidae* excrement, *Carici-Festucetum sulcatae*; normal light. 4. The same slide in polarized light showing the mineral particles thoroughly mixed up with organic matter. Enlarged: 1—4: 30×.

Plate 15. 1.—2. Effect of soil microflora on the weathering of parent rock. Big dark spores of soil fungi in the cavities of limestone formed by fungous hyphae activity. 3.—4. Plant root as an important source of organic matter in the soil. Some roots (yellow cross-sections) showing animal pellets in the parenchyma tissues. Enlarged: 1—2: 80×, 3—4: 40×.

Plate 16. Different types of mineral particle incorporation into the soil matrix (organic matter black, mineral particles coloured or white glistening). 1. Protorendzina with free laying bigger mineral particles. 2.—3. Moderrendzina with small mineral particles incorporated inside the stable excrements of *Diplopoda* (2) and *Isopoda* (3). 4. Mullartige rendzina, bigger and smaller mineral particles of different sizes and finely disintegrated organic matter forming the highly developed soil matrix of the *Lumbricidae* excrements. Enlarged: 1, 4: 80×, 2: 75×, 3: 30×.

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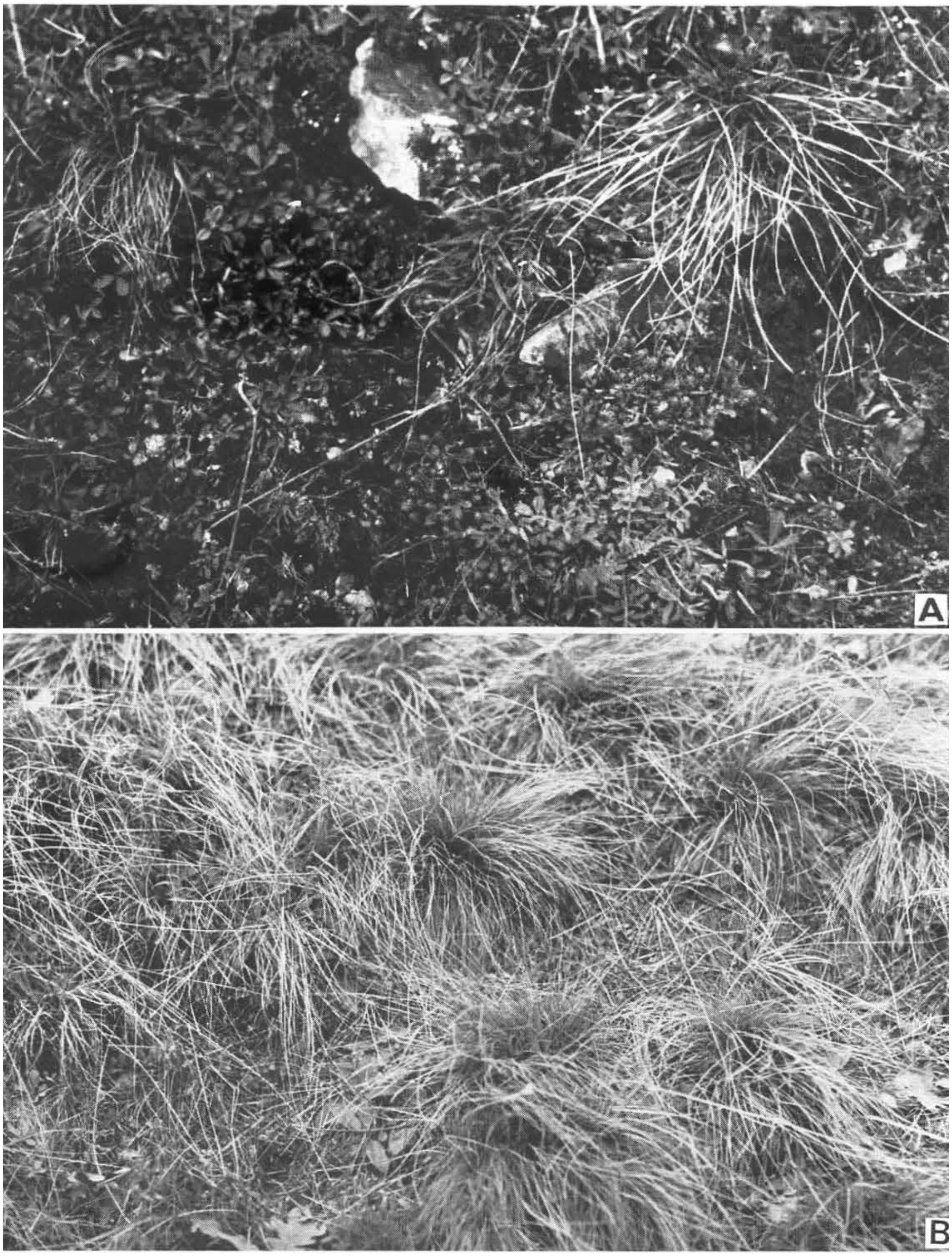
Plate 1

Plate 2



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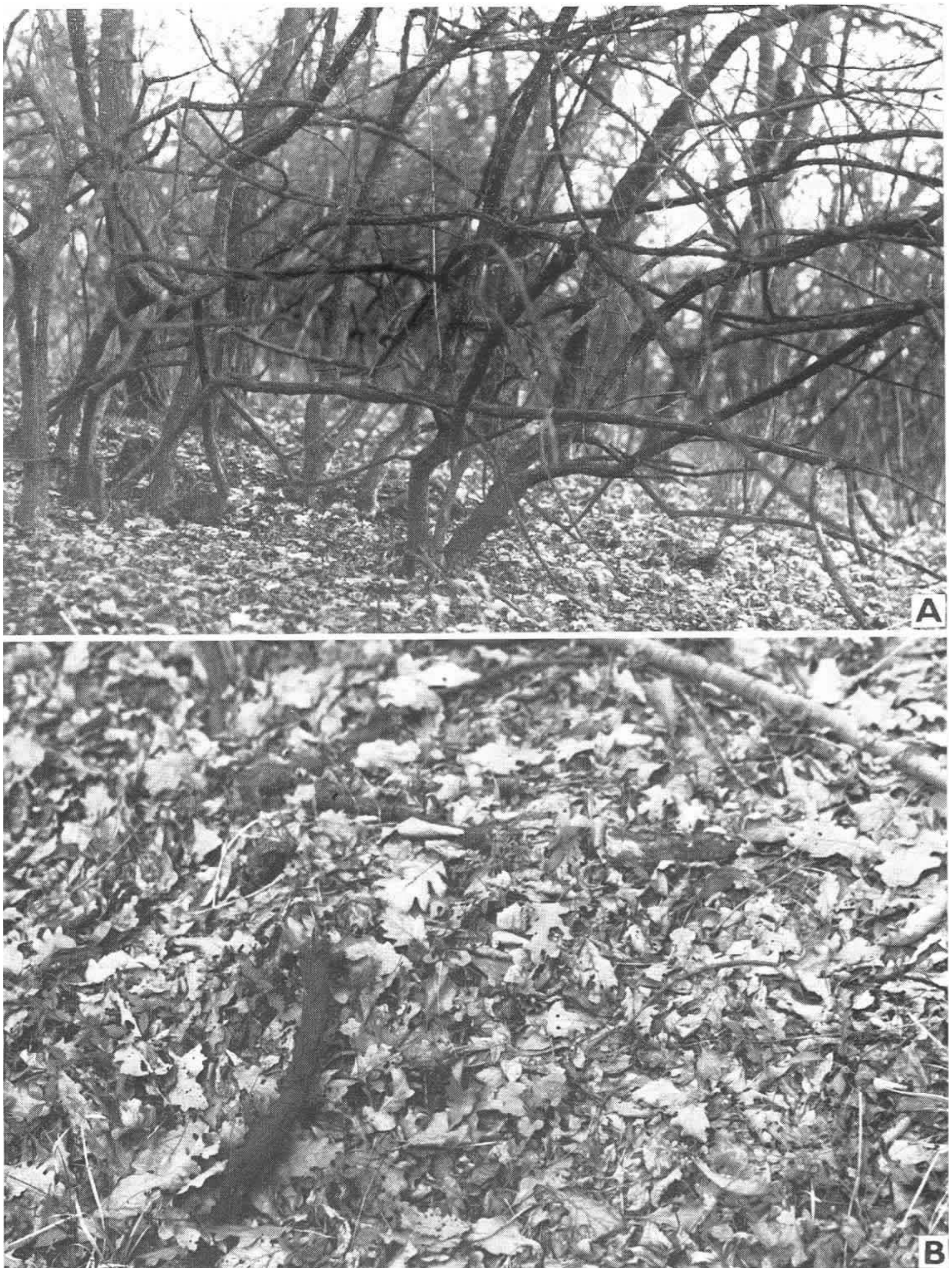

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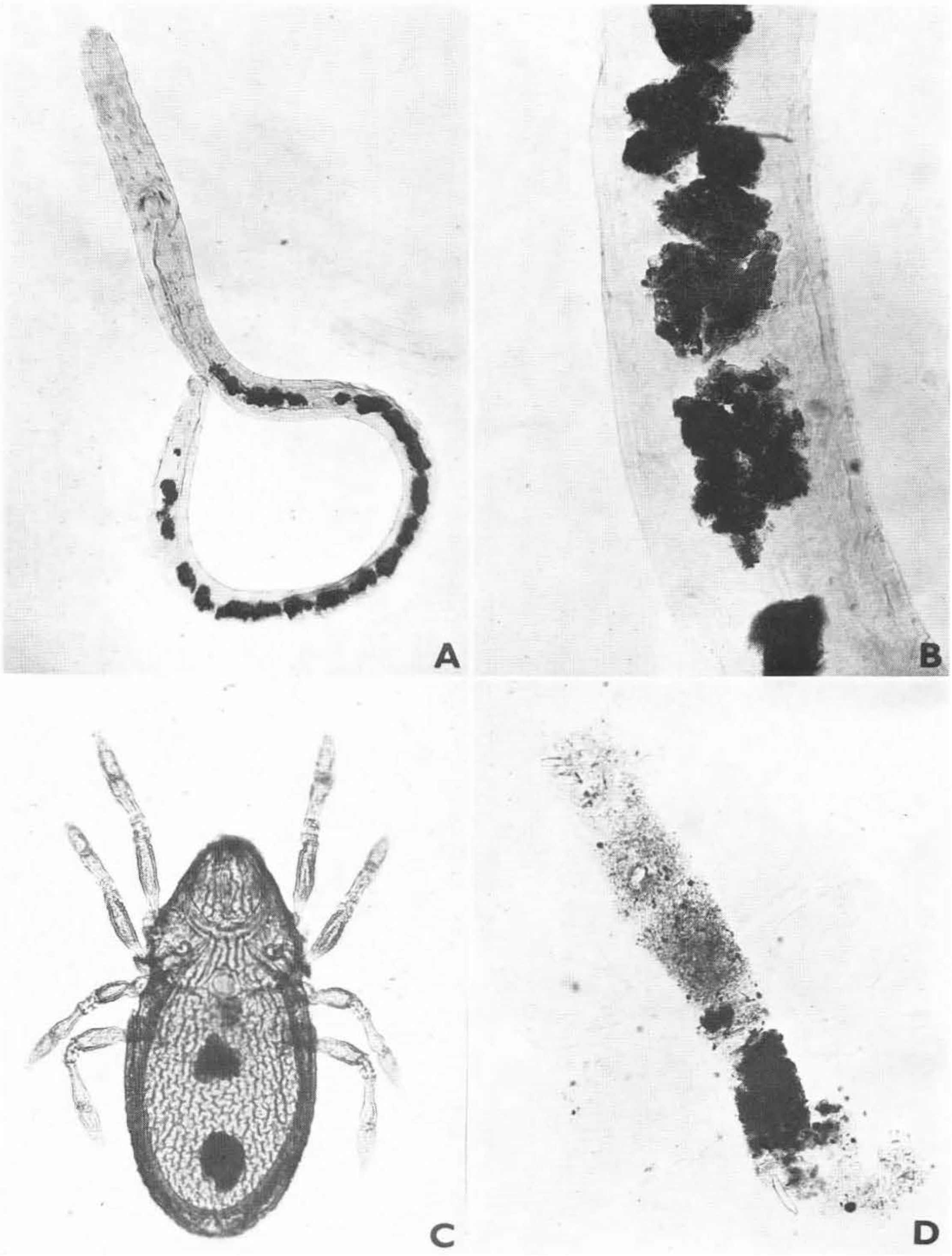

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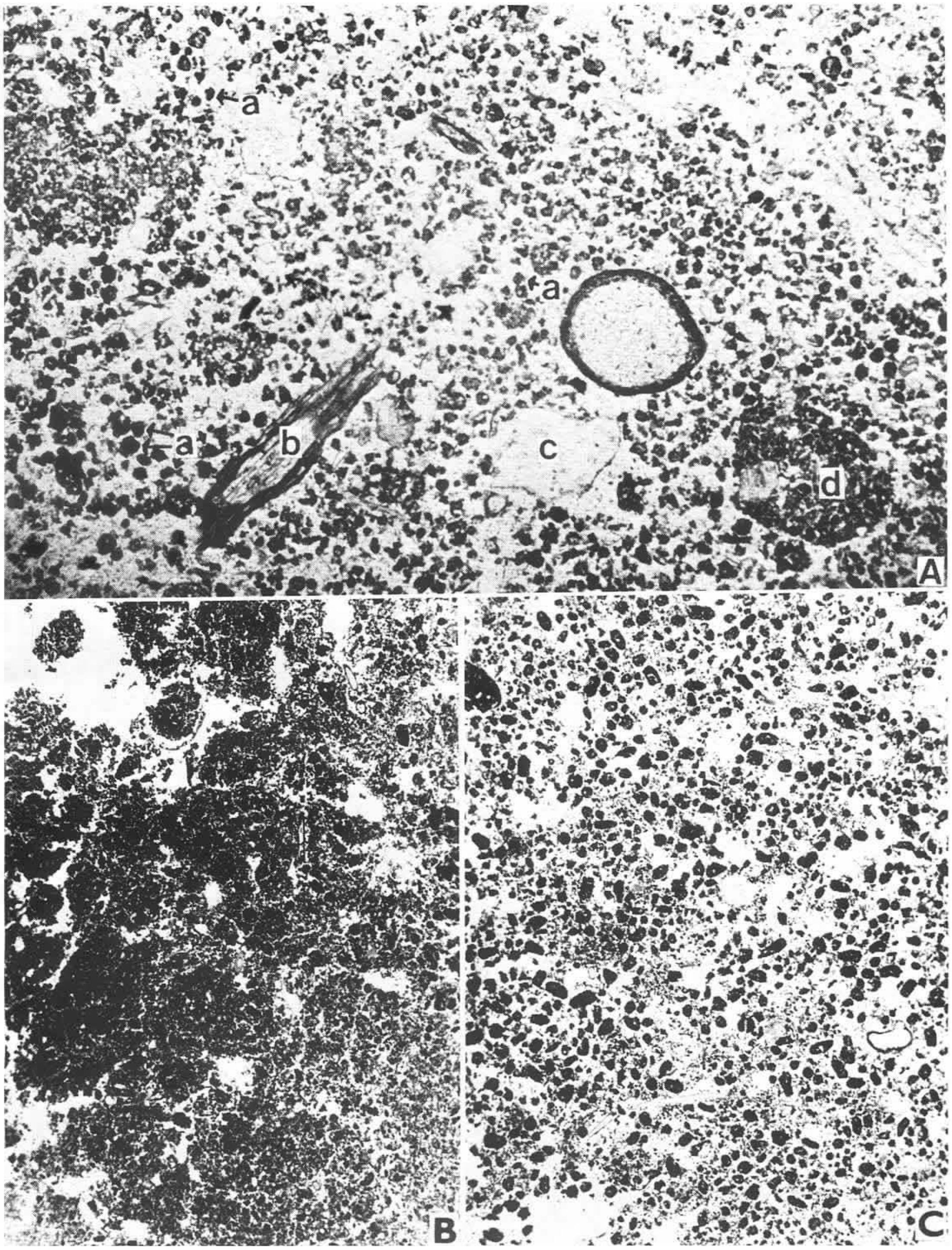

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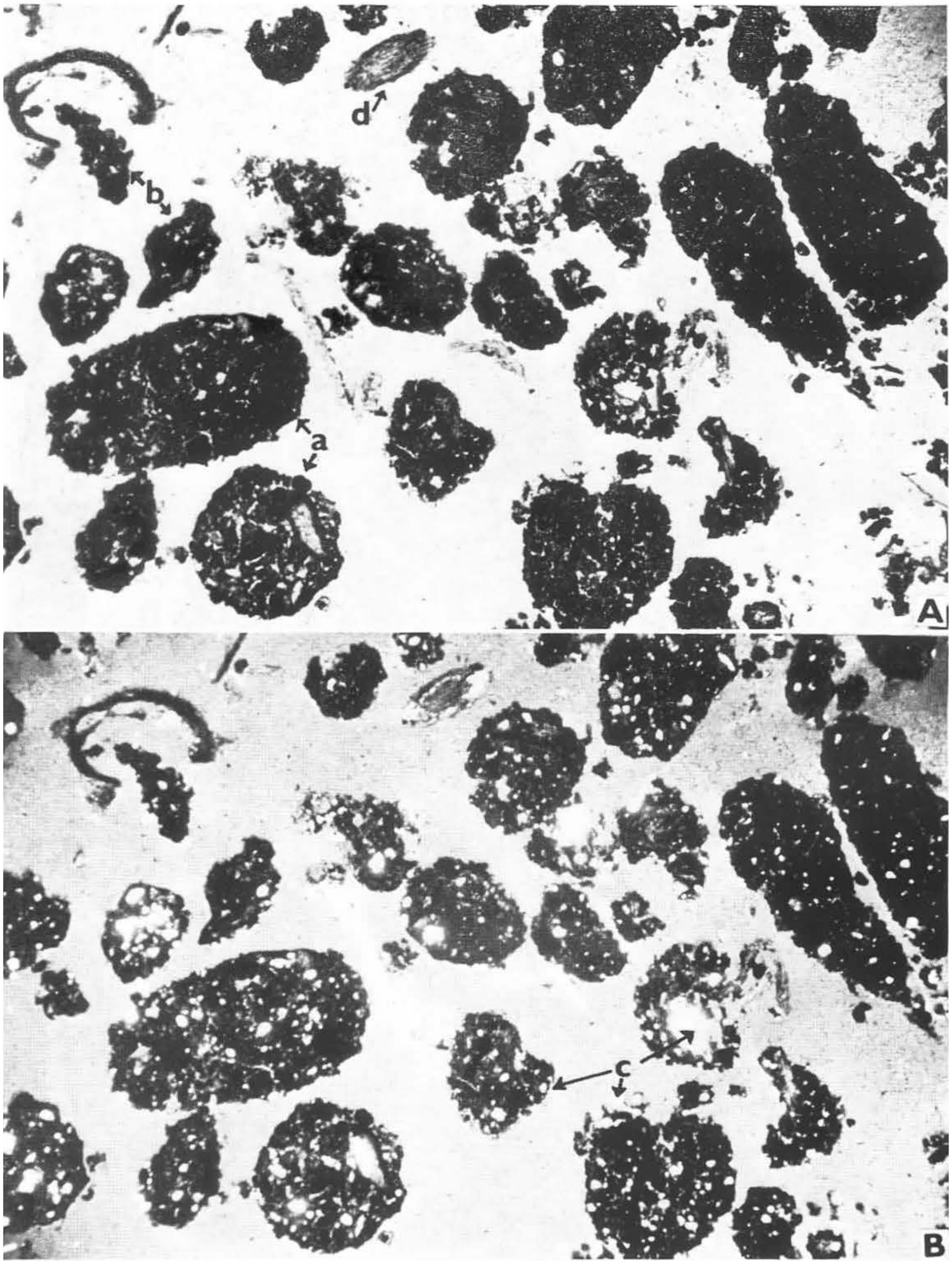

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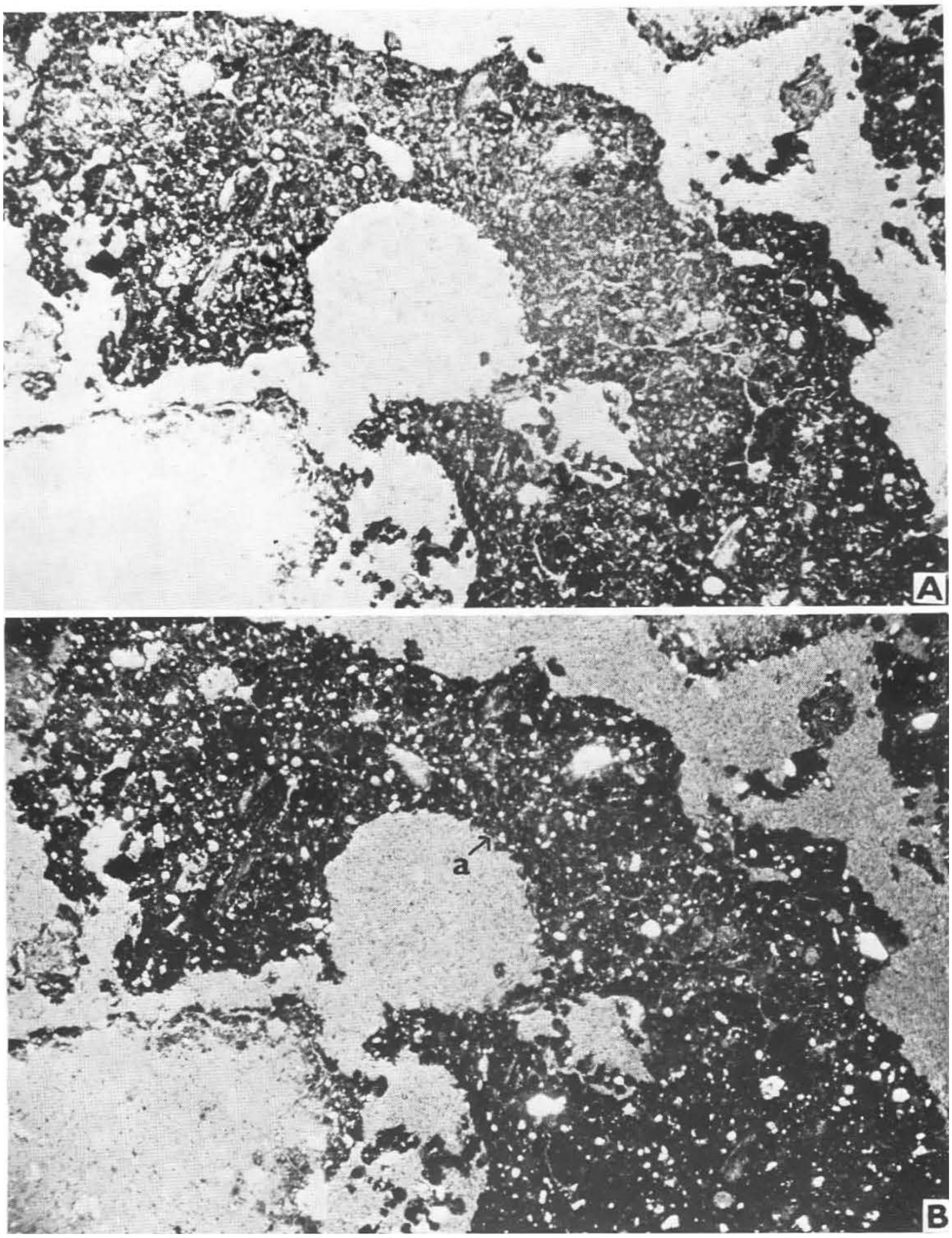

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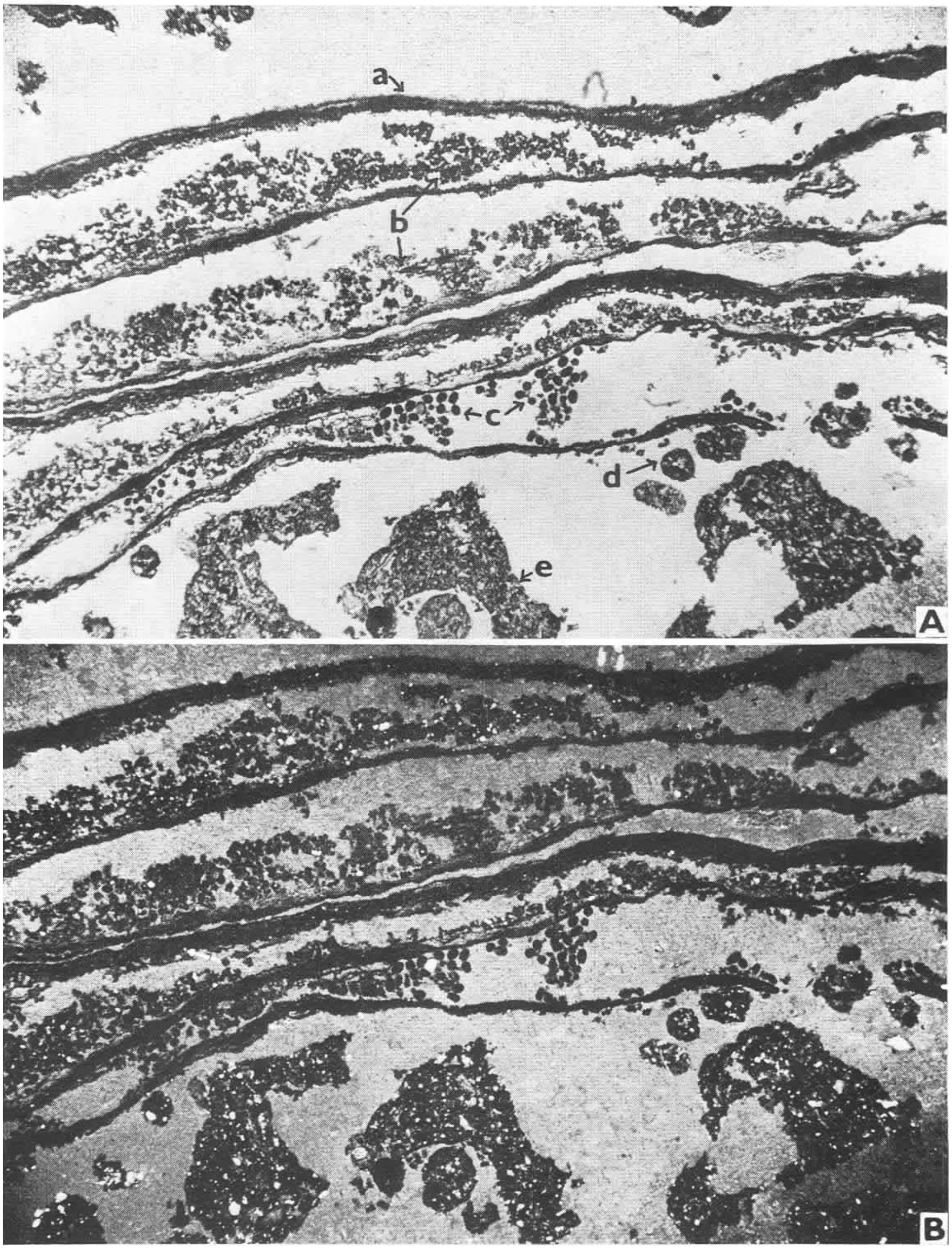

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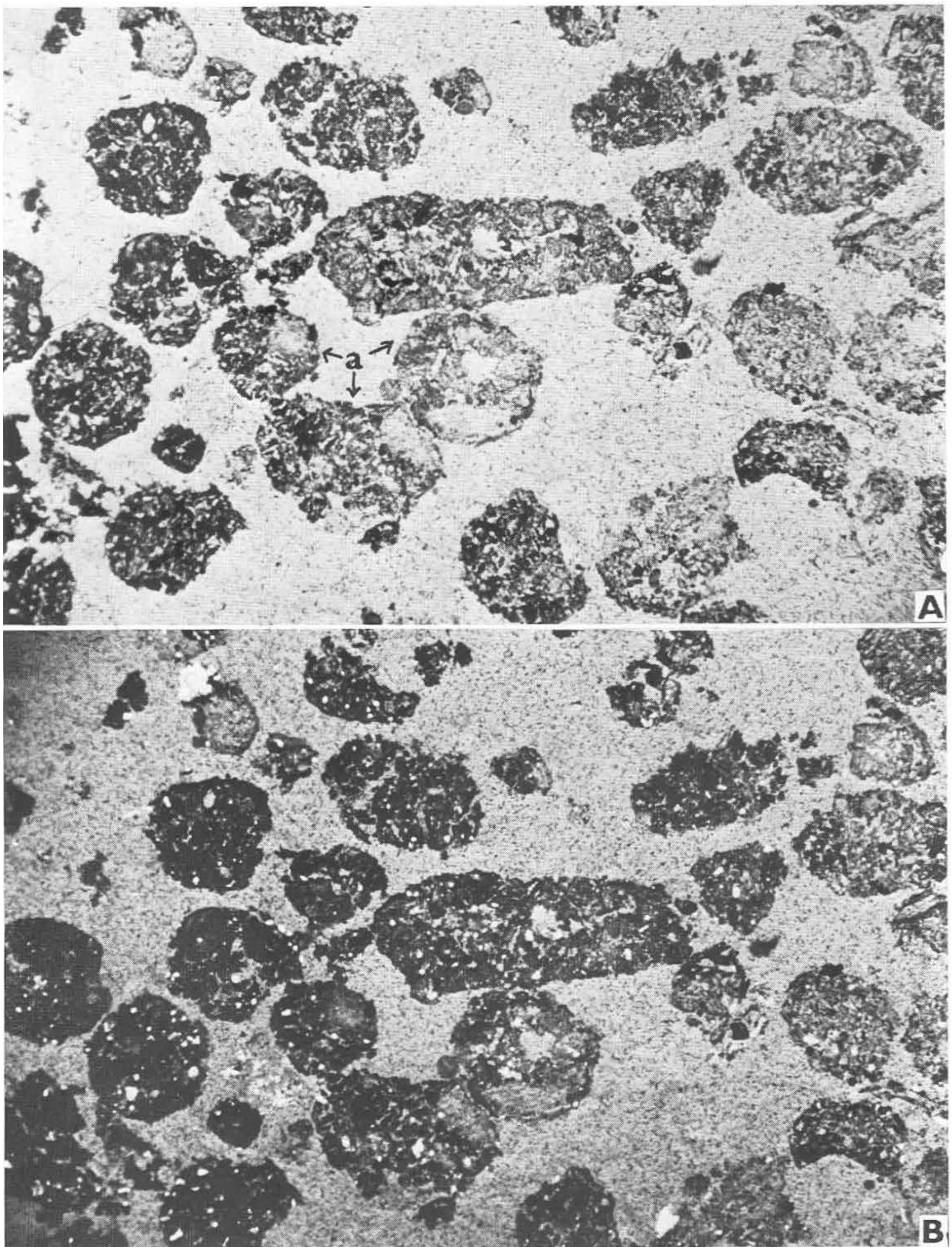

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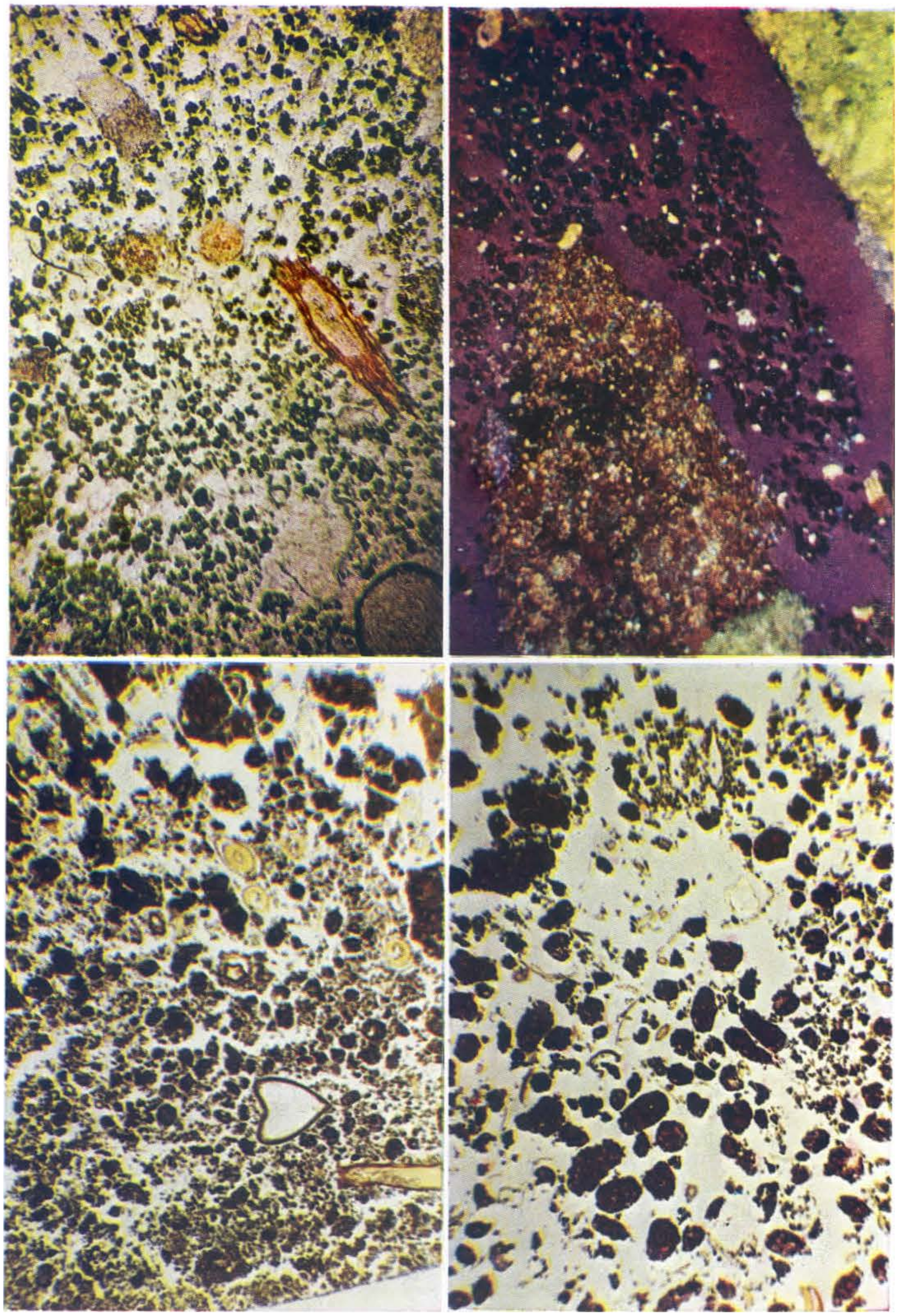

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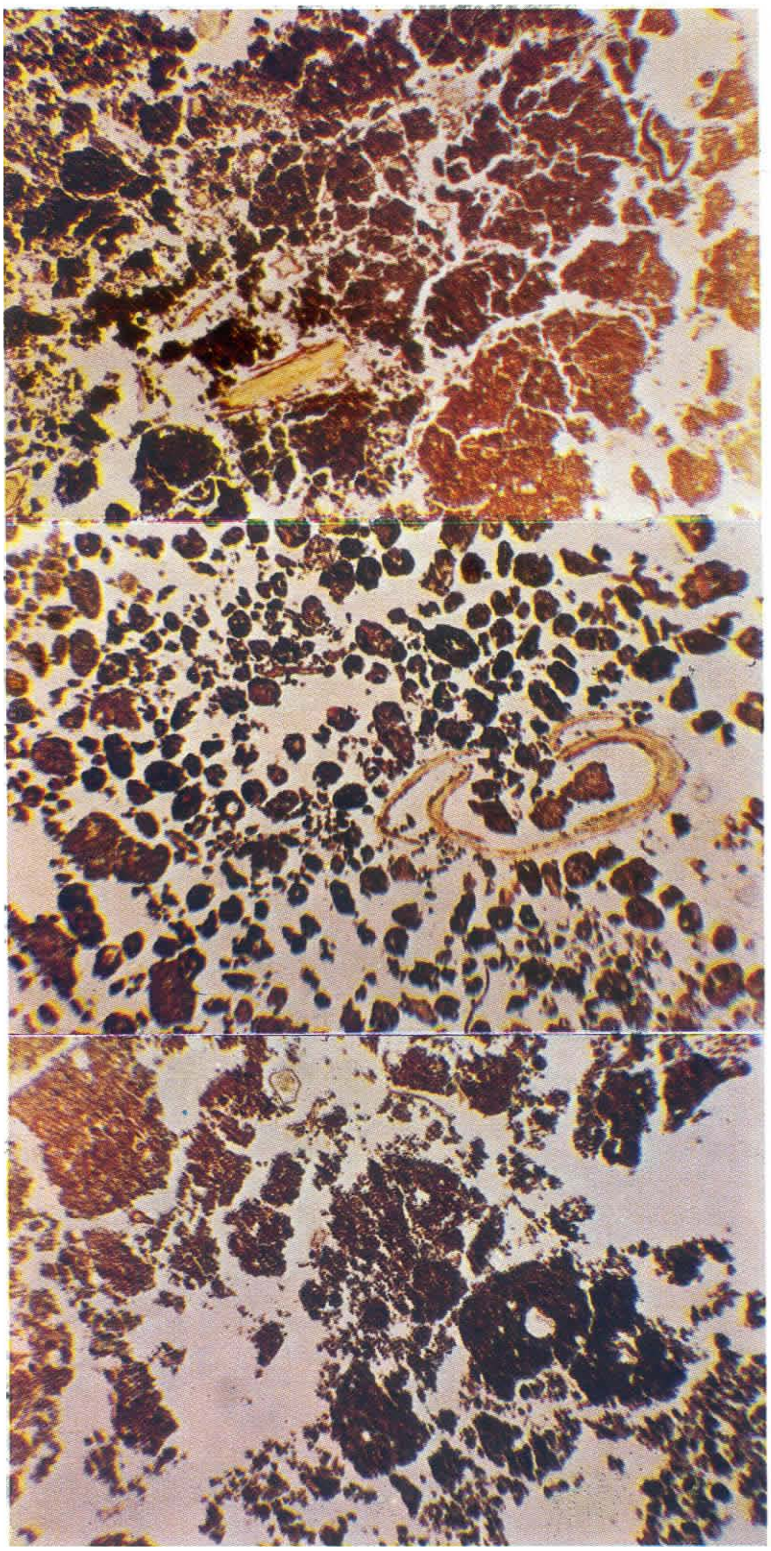

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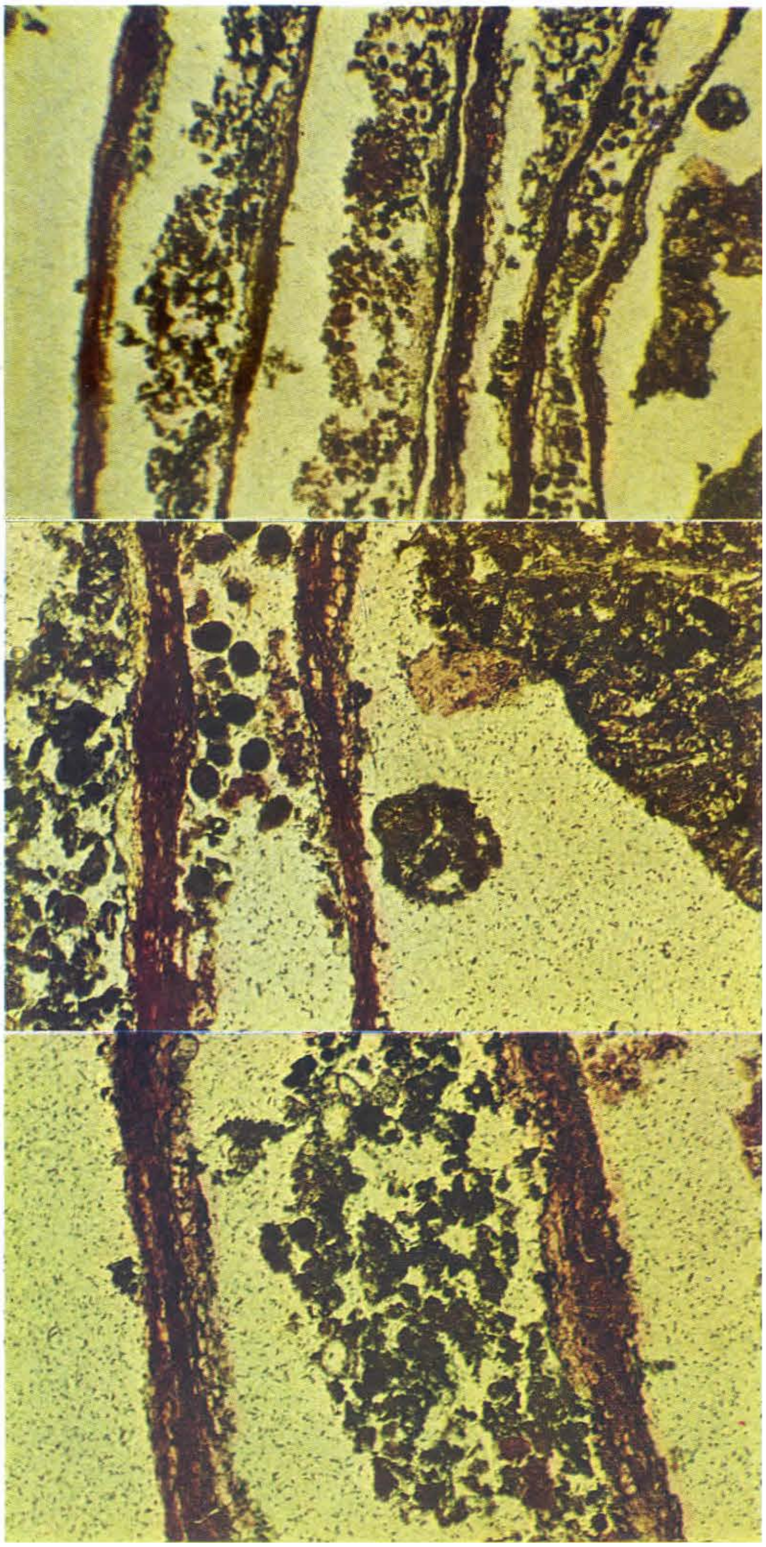

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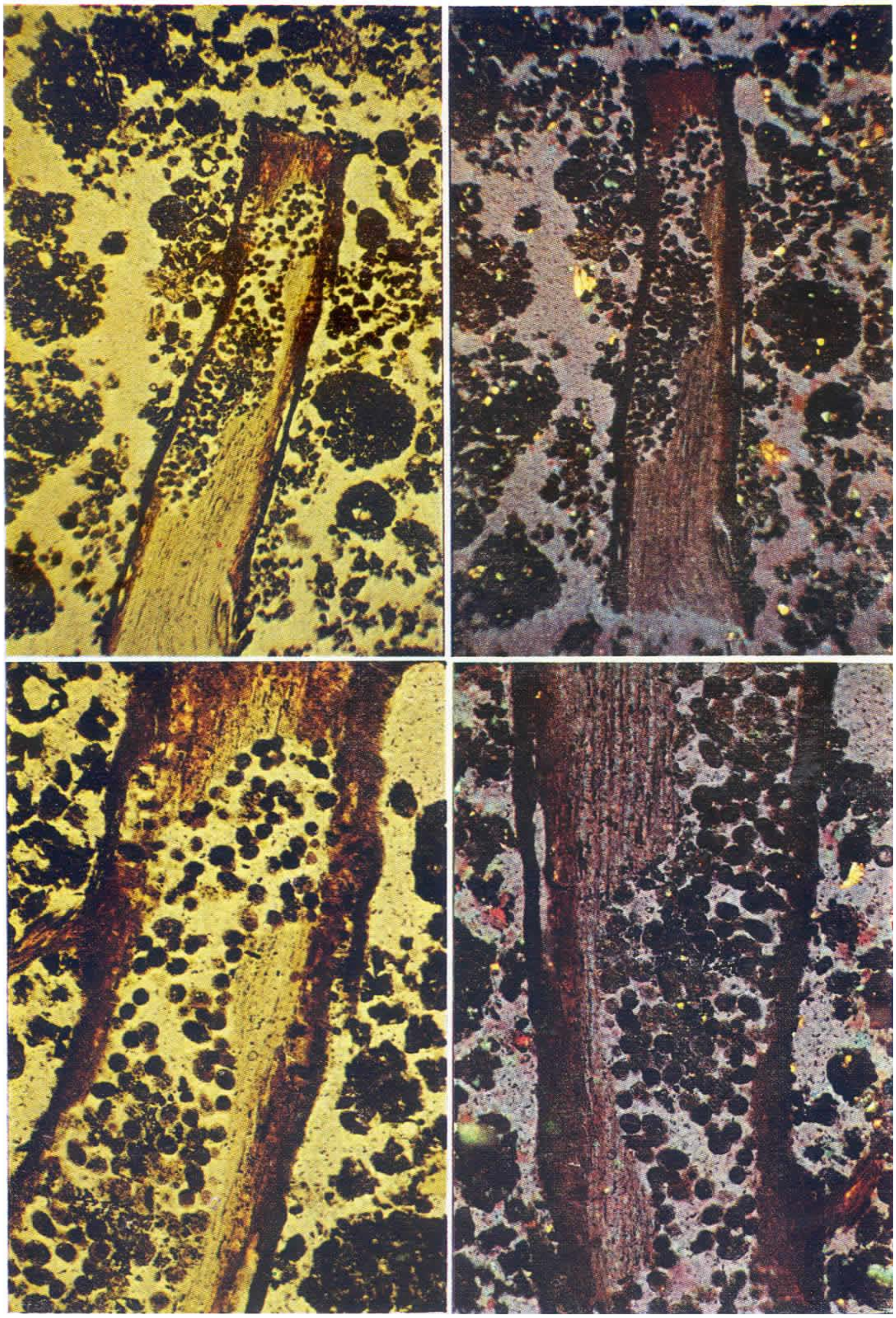

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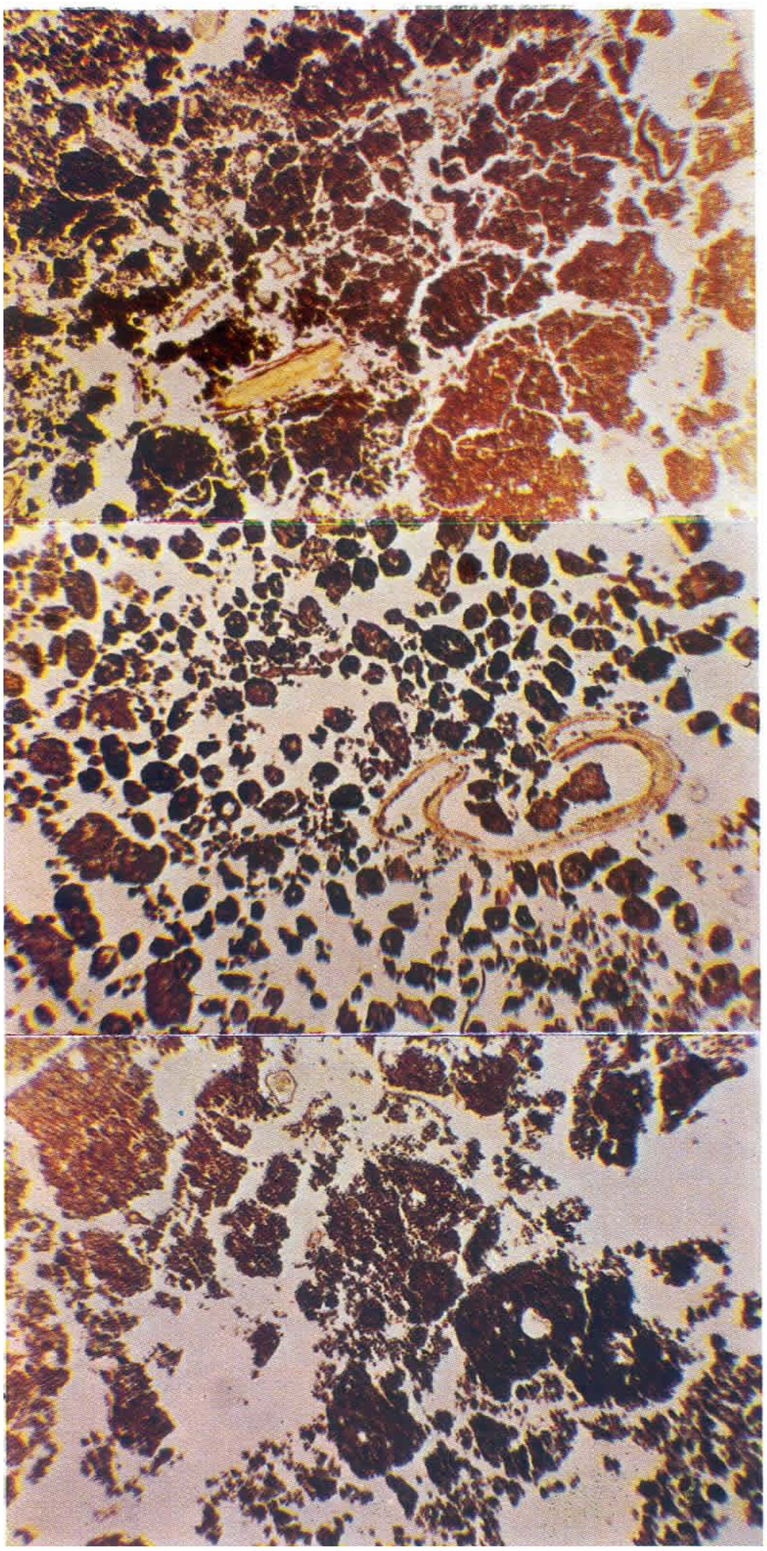

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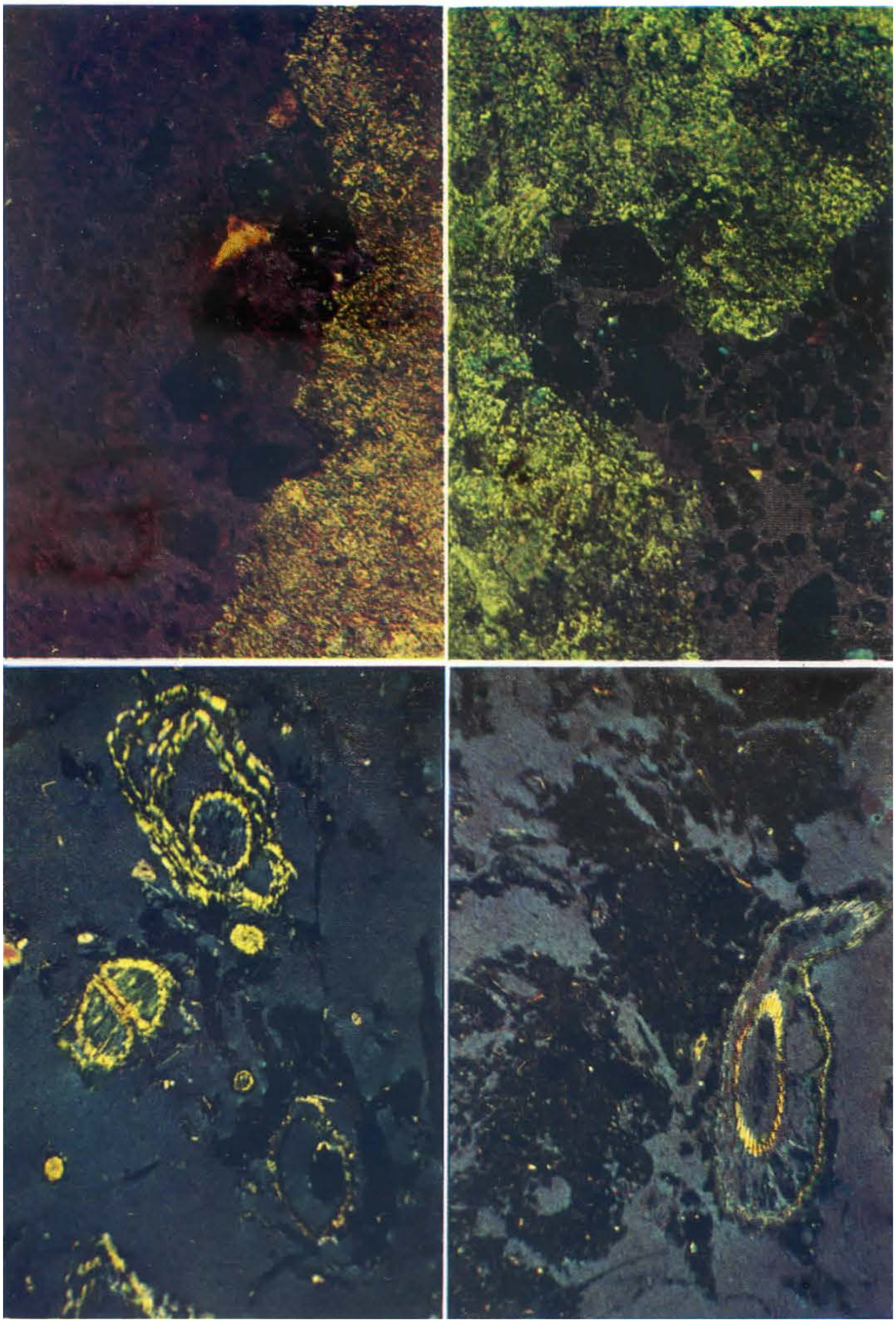

Plate 16